# Sunbird pollination and the fate of strong contributors to a mutualistic network in a West African Montane Forest

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## LIST OF ABBREVIATIONS

1. CLSB ----------Collared sunbird
2. COSB ----------Copper sunbird
3. CR ----------Critically threatened
4. EBA----------Endemic Bird Area
5. FVN ----------Flower visitation network
6. GHSB ----------Green-headed sunbird
7. GMT ----------Greenwich Meridian Time
8. GPS ----------Geographic Positioning System
9. GRSB ----------Green sunbird
10. IBA ----------Important Bird Area
11. IBM ---------- International Business Machines
12. IS ----------Interaction strength
13. IUCN ----------International union for the conservation of nature
14. LC ----------Least Concern
15. LR ----------Lower Risk
16. NDSB ----------Northern-double collared sunbird
17. NMFP ----------Nigerian Montane Forest Project

18. NODF----------Nestedness based on overlap and decreasing fill

19. NSI ----------Node Specialisation Index

20. OTSB ----------Orange tufted sunbird

21. PSI ----------Pollination Service Index

22. PTN ----------Pollen transport network

23. PYSB ----------Pygmy sunbird

24. SPSB ----------Splendid sunbird

25. SPSS ---------- Statistical Package for Social Science

26. SVD ----------Single visit deposition

27. VSBD ----------Variable sunbird

28. VU ----------Vulnerable

## LIST OF APPENDICES

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## DEDICATION

I dedicate this thesis to the memory of my father,

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## ABSTRACT

The survival of most species depends on their network of mutualistic partnerships with other species. Network structure - the pattern and arrangement of species in a given interaction, can reveal predictable outcomes on the fate of species and network stability. Therefore understanding what makes networks stable is extremely important. However current investigations into network stability have mainly been through theoretical and simulation studies and often based on data from plant-insect visitation networks. Empirical testing is now imperative and networks other than just plant-insect ones need to be incorporated into such studies. Moreover, the use of visitation frequency as a proxy for pollination frequency in plant-pollination network studies needs to be evaluated.

In this thesis, I tested theoretical views and models on network structure and species survival using empirical data from a sunbird-tree pollination network in a remote montane forest reserve in Nigeria. First I investigated how changing landscapes and habitats affected sunbird distribution in the reserve. Secondly I compared a sunbird-tree *visitation* with a sunbird-tree *pollination* network to determine how good a proxy bird visitation is for bird pollination. Two network properties which affect network stability and underpin this work are i) connectance/ interaction strength and ii) nestedness. I examined how species relative abundance influences their interaction strength in the network and whether a species contribution to nestedness determines its survival probability. This latter point was of special interest as theoretical studies on networks have suggested that species which contribute the most to nestedness are most prone to extinction, which seems counterintuitive.

The visitation frequencies of sunbird species on flowers of as many tree species as was logistically possible were observed, and sunbird species were trapped to determine the amount of pollen they transported. Using these data, I developed the flower visitation (FVN)

and pollen transport networks (PTN). To determine how FVN reflects PTN, I compared the two networks using null models that controlled for species' degree (number of links) and network size. Differences in observed nestedness differed significantly from null model expectations. I worked out an extinction proneness based on IUCN criteria for determining species at risk of extinction using rarity as a measure of vulnerability. An assessment of species abundance and diversity in the reserve and nearby fragments provided the standard for risk categorisation and evaluation of species' robustness to changing landscapes.

FVN correlated positively with PTN, despite 64 % dissimilarity in species composition. The PTN had fewer species than FVN, but was more nested and specialised than the FVN, indicating that analyses of FVN often overestimate pollination through the inclusion of interactions with variable effects such as nectar robbing and insectivory. Although some species were relatively stronger interactors in both networks, the strongest contributor for FVN was not the strongest for PTN. FVN is therefore an inadequate predictor of efficient pollinators and a poor reflection of PTN. Abundant species had a higher interaction strength overall. Strong contributors to nestedness were the rare species, which explains why they are more prone to extinction. In my empirical network, nestedness will decrease overall through the loss of rare species, but in accordance with network theory, this will not collapse the network, because it is the abundant species with the most links which maintain network stability. Although fragmentation is not yet a challenge to sunbird distribution, anthropogenic disturbance such as indiscriminate burning of grassland to stimulate re-growth, may alter crucial habitats for sunbird survival.

# CHAPTER ONE

## General introduction

### 1.0: Introduction

Interactions between plants and animals are a common feature of most ecological systems (May, 1972). Historically more focus has been placed on understanding antagonistic interactions among species, such as parasitism and predation (Bronstein et al., 2003; Lawton, 1978; Price et al., 1980; Tscharntke et al., 2007; Tylianakis et al., 2007; Zavaleta et al., 2001) than on mutualistic ones. However mutually beneficial interactions between species such as plants and their animal pollinators or seed dispersers are crucial to the maintenance of community structure (Bastolla et al., 2009). Most mutualistic interactions are bipartite (involving two groups), with participants (species or individuals) from one group benefitting through interactions with participants from the other group. The most studied mutualistic interactions are between plants and pollinators. In this interaction the animal receives nourishment from the plant, and in return enhances reproductive fitness of the plant through pollination.

Early work focused on understanding species specific plant-pollinator interactions, (e.g. Ahmed et al., 1989; Baker & Harris,1957). More recently, plant- pollinator mutualisms have been explored at the community level using food web and interaction network analyses (Bascompte et al., 2003; Bronstein et al., 2003; Memmott et al., 2004; Rezende et al., 2007). These approaches aim to describe all plant-pollinator interactions within a community and allow the quantification of species contributions to the network. They enable the exploration of questions around species coexistence; for example, how species interactions maintain and/or promote biodiversity (Bascompte & Jordano, 2007; Bascompte et al., 2003; Bastolla et

al., 2009), the impact of invasive species on ecological networks (Lopezaraiza-Mikel et al., 2007; Nielsen & Bascompte, 2007), interaction asymmetry (Stang et al., 2007; Vazquez et al., 2007) and the consequences of species addition and/or loss to community stability (Saavedra et al., 2011). In addition, it has been suggested that some network properties (e.g. nestedness and connectance) can be easily incorporated into conservation monitoring (Tylianakis et al., 2010) and could potentially shift emphasis from species based conservation to the conservation of networks of interacting species.

Our understanding of networks has so far mostly come from the use of null models and computer simulations (e.g. Bascompte, et al., 2003; Saavedra et al., 2011). These approaches have been used to investigate network properties (James et al., 2012; Stang et al., 2007; Staniczenko et al., 2013) and answer questions around network stability. For example, which species in a network can be lost (go extinct) without collapsing the network and which species are crucial for network stability? By simulating extinction probabilities of strong versus weak contributors to networks, Saavedra et al. (2011) explored the fate of strong contributors to overall network persistence. They found that species contribute differently to the overall structure of the network and that strong contributors to networks do not gain individual survival benefits. On the contrary, they are species most vulnerable to extinction. These conclusions introduced a new paradox into the study of persistence of mutualistic networks and have generated much debate (James et al., 2012).

First, I have structurally described both a sunbird-tree visitation network and a sunbird –tree pollinator network in a geographic locale (a Nigerian Montane Forest) where there is an extremely scarce record of mutualistic networks between plants and their pollinators (Kaiser-Bunbury et al., 2009). Within these networks, I have determined the strong and weak contributors, based on visitation frequency and quantity of pollen transported by each

pollinator (sunbird species). I have also assessed strong and weak contributors in terms of two network properties i) nestedness (a pattern formed when animal species with few partners tend to pollinate plant species that are subsets of those pollinated by animal species with more partners and ii) connectance (the number of links (plants) that a pollinator interacts with in a given network). I then investigated the fate of these species, in order to test the findings of Saavedra et al. (2011) that strong contributors to nestedness are most prone to extinction.

Secondly, most plant- pollinator network theory has been developed based on insect-plant networks (Alarcón, 2010; Memmott, 1999; Vázquez et al., 2012) and the assumption that visitation frequency is a good proxy for pollination frequency. By using a sunbird-tree network, I was able to test the generality of conclusions drawn from insect only networks and the accuracy of assuming that visitations equate to pollinations (at least in my network). Rather than consider every visitor as a pollinator, I incorporated flower visitation frequency and pollen load). I defined a pollinator as a sunbird that visits a flower and also transport its pollen. I was able to compare the *effectiveness* of different pollinators by comparing their pollen load estimations and visitation frequency. In addition, I excluded non-pollinating visitors from my model, i.e. species with low visitation rates and/or little or no trace of pollen on their bodies.

One potential problem with my network is that it is smaller than most insect-plant networks that have been used to develop network theory. However, using a simple sunbird pollinator - tree species model with fewer species enabled me to more accurately and critically examine the bipartite architecture. In addition, by testing basic network theory using a smaller network, I can confirm whether or not these theories also hold true for smaller networks and are thus invariant to network size.

I have been able to decipher the structural framework of my network in terms of nestedness and connectance and provide a biological explanation for the paradoxical conclusions of Saavedra et al. (2011) (see above). Therefore through this work I have increased our understanding of interaction networks and the potential implication for species coexistence and survival.

My review of related literature on biotic pollination introduces key concepts such as *mutualistic interactions*, *interaction networks*, *nestedness*, *interaction strength*, and *connectance*, which are integral to subsequent chapters.

**1.1: Mutualism**

Mutualistic interactions are very common in nature (Bronstein, 2001; Stachowicz, 2001). Although frequently viewed as obligate, pair-wise interactions (Bronstein & McKey, 1989; Doebeli & Knowlton, 1998; Holland et al., 2011), mutualisms often involve multi-species guilds of contributors (mutualists) competing for access to one or more partner species (Palmer et al., 2003). Network theory has enhanced pollination biologists' ability to study community wide patterns of species interactions.

There are several explanations for the difficulties associated with understanding mutualistic interactions and their networks. Below I discuss one reason that potentially constrains my definition of *pollinators* in the context of their mutualistic role in this study.

Past experimental and theoretical investigations example (Stanton, 2003; Thomson, 2003) have shown that many mutualisms are conditional and the exact relationship between, e.g. plant and pollinator will vary depending on environmental and or biotic variables (Carvalheiro et al., 2011). For example, a pollinator can switch from acting as a mutualist to a parasite/antagonist following the introduction of a single, more efficient pollinator to an

ongoing interaction or network and this dramatic change can occur without alteration in the behaviour of the initial partner (Thomson, 2003). This might happen if, for example, the initial partner was inefficient as a pollinator (pollen waster), but inadvertently pollinated at a higher cost to the host (pollen wastage). The introduction of an efficient pollinator (lower cost: less pollen wastage) makes the inefficiency of the former relatively detrimental. Thus, inter – species associations that are mutually beneficial in the presence of one or more species may become neutral or harmful in the presence of another (Bronstein, 1994; Connor, 1996; Fukui & Yamauchi, 2011; Knowlton & Rohwer, 2003). This uncertainty makes it difficult to identify a true mutualist (pollinator) and creates problems in the understanding of mutualism generally.

### 1.2: Ecological interactions and network approach in plant pollinator interactions

Network refers to a set of inter-connected units (species) linked together to form an integrated and functional system. Ecological interaction networks refer to the functional (the roles of each species in the network) and structural patterns (i.e. link configuration) formed when species share common resources, e.g. in pollination networks, floral visitors (for plants) and nectar or pollen (for animals). Community ecologists employ an interaction network approach to visualise and study relationships among species across and within trophic levels (Bascompte et al., 2003). Such relationships are commonly presented as ordered bipartite *S* x *T* matrices; where *T* plants and *S* animals indicate species within a community that potentially interact.

Pollination interaction networks are usually intricate, with species, tightly connected to one another, either directly or indirectly (Montoya et al., 2006; Montoya & Solé, 2002). These direct and indirect patterns of closely linked species common in most ecological networks result in a “nested” structure (Bascompte et al., 2003). By nestedness I mean that, the links

maintained by the most specialised nodes (species) tend to be a sub-set of those kept by the most generalised ones (Figure 1.2).

The size and structure of interaction networks are a function of a species' relative abundance, its life-history traits, as well as its morphological and behavioural traits (Baldock et al., 2011; Bascompte et al., 2003; Waser, 1987). These three variables (species abundance, life-history traits, and morphological/behavioural traits), provide the background for evaluating key properties of a plant-pollinator network such as nestedness, interaction strength (per species effect on another) and connectance. These properties are discussed in detail in the section below.

### 1.3: Network properties: contemporary issues and application

Several network properties are used in contemporary description and analysis of complex ecological networks though their interpretation can be controversial (James et al., 2012; Ulrich, 2009; Ulrich & Almeida-Neto, 2012). I discuss the major properties of interaction networks and the issues/controversies surrounding their application to ecological network analysis.

#### 1.3.1: Nestedness

The concept of nestedness was first applied in the study of bio-geographic patterns of species occurrence in islands and fragmented landscapes (Patterson & Atmar, 1986). A nested pattern was found when the species composition on islands with fewer species was a proper sub-set of those species on islands with more species.

Nestedness is also found in species interaction networks. Such networks are usually described through the creation of presence-absence matrices. This begins with the creation of a table where, for example in a sunbird-tree pollination network, the top row describes all the

sunbird species and the first column, all the tree species. Every time a sunbird species interacts with a plant species, 1 is added to the table which is represented by a grey or shaded box (Fig 1.1). This leads to a bipartite network (Bascompte & Jordano, 2007). If the network is highly nested then the specialist species interact with species that form well defined subsets of the species with which common/generalist species interact (Fig 1.2). The nestedness pattern comes from the distribution of presence and absence data within the bipartite matrix. A matrix is nested if, after being packed, all the presences stack together as do the absences (Fig 1.2).

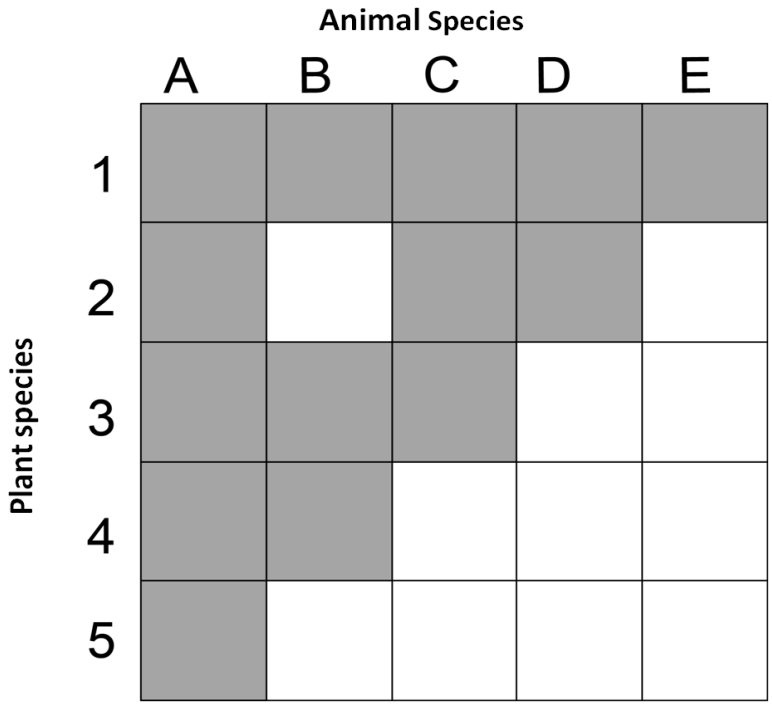



Figure 1.1: Interactions between pollinators and plant species, where shaded boxes indicates an interaction. Empty boxes indicate no interaction. This is a hypothetical example of a binnary network, and does not account for the frequency of interactions. All realised interactions are of the same magnitude (same shade of grey), but see figure 1.2 below.

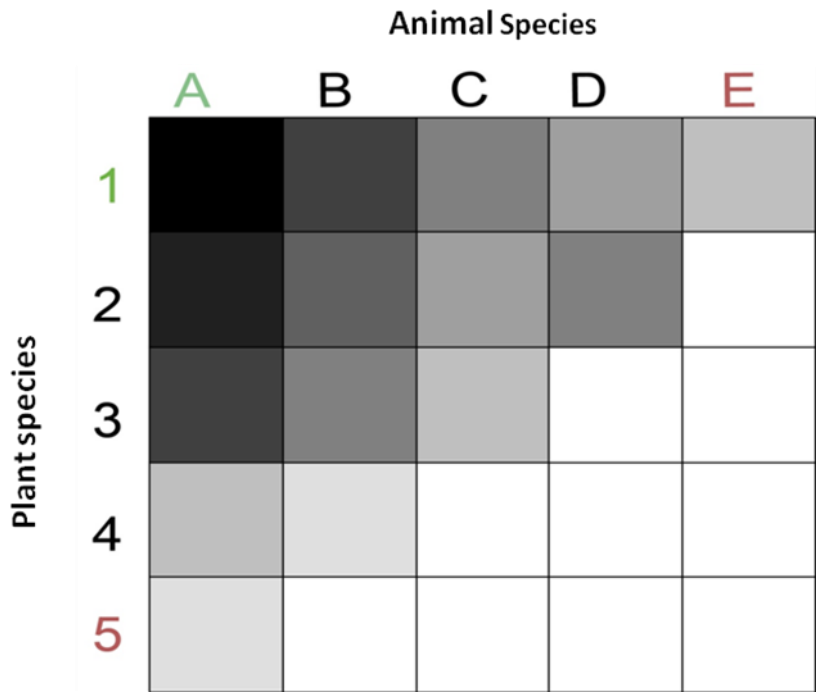



Figure 1.2: Nestedness table with presences in grey and absences in white. Note how the presences stack in the top left section while the absences in the bottom left section. Species highlighted in red and green are specialists and generalist species respectively. The depth of the shaded boxes represents the frequency of interactions between plant species and animal species. Empty boxes indicate no interactions. This is a hypothetical example of a weighted network (derived from cumulative frequencies of interactions).

A nested pattern is believed to promote biodiversity through facilitation of co-existence and reduction of competition within a guild of mutualists (pollinators for example) (Bascompte et al., 2003; Saavedra et al., 2011).

### 1.3.2: Measuring Nestedness

Nestedness has been quantified by several different indices calculated using a matrix of interactions (Almeida-Neto et al., 2008). An early metric developed by Atmar & Patterson (1993) was T (the matrix temperature measure). This metric determines how the observed

presence –absence arrangement in the table deviates from the arrangement given by an isocline describing a perfect nestedness benchmark (Almeida-Neto et al. 2008). Unexpected absences and presences in the upper-left and bottom-right sides respectively are weighed by their squared *Euclidian* distances from the isoclines. However, despite the fact that this metric is one of the most used, its application is limited by its lack of flexibility and controversial statistical derivation (Ulrich, 2009). Nevertheless, several different metrics based on similar statistical/logical arguments derived from different permutations around the basic presence-absence table have been developed and tested. These metrics are: 'C', developed to estimate nestedness only between rows (Wright & Reeves, 1992), and (d) the discrepancy measure (Brualdi & Sanderson 1999). A major drawback of "C" and (d) is that they often overestimate nestedness (see review by Almeida-Neto et al. 2008).

Almeida-Neto et al. (2008) stimulated the development of a new metric based on two properties of bipartite networks which had been ignored previously by older metrics, decreasing fill and paired overlap; "NODF" (Nestedness based on Overlap and Decreasing Fill). NODF allows for the quantification of nestedness using traditional presence –absence data or abundance data (Almeida-Neto & Ulrich, 2011). NODF is particularly valuable for my study as it calculates nestedness independently among rows (plant species) and among columns (pollinator species).

### 1.3.3: Interaction strength

Interaction strength (IS) broadly describes the magnitude of effect of one species on another in an interaction network (Vazquez et al., 2007). In the context of plant-pollinator interactions, interaction strength refers to the per-interaction contribution of a species to the reproductive output or wellbeing of another species, relative to the combined contribution of

all species (Ulrich, 2009; Vazquez et al., 2007). We often rely on imperfect surrogates to infer IS (Wootton & Emmerson, 2005). Despite these discrepancies, effort is being made to unify statistical approaches towards the derivation and interpretation of IS. This is important because at the moment network theory offers no alternative concept with better explanatory power (but see Berlow et al., 1999; Wootton & Emmerson, 2005). Until this is achieved the implication of IS to the persistence and stability of ecological networks and communities will remain a matter of conjecture and debate.

Apart from the questionable nature of current metrics, assessment of IS is also confounded by the subjective nature of what constitute the unit for quantification of strength (i.e. what is being measured). For instance, some studies have measured IS based on one species' ability to contribute fitness (e.g. Vazquez et al., 2012), others looked at the frequency with which one species visit the other (Stang et al., 2006; Vazquez et al., 2007). These contextual differences pose a challenge and should encourage us to be explicit regarding what we measure and to be careful with conclusions that presume a species identified as a weak contributor based on one metric (for e.g. nestedness), is generally less-crucial or weak across all metrics (Berlow et al., 2004), see also (Berlow, 1999; McCann, 2000).

Most calculations of IS are influenced by a species' relative abundance (Vazquez et al., 2007). Rare species tend to have a weak IS while common species have a strong IS. In plant-pollinator systems, a pollinator's contribution is not just a function of a species' inherent abilities. It is also controlled by a horde of factors, including specialisation and generalisation of preferences, spatio-temporal variation in pollinator/host abundance (Petanidou et al. 2002; Vazquez et al., 2007; Vazquez et al. 2009) and /or a species' degree (Stang et al. 2006). In whatever context an evaluation is based, species relative abundance underpins an assessment of IS.

### 1.3.4: Connectance

Connectance in interaction networks is twofold. Network level and the species level connectance. At the network level, connectance is the proportion of possible links that are realised, (i.e. the proportion of the matrix that is filled). Connectance at the species level describes the number of links per species or individuals in a given interaction network and is believed to be the main determinant of species/network persistence (James et al. 2012). Connectance ensures an increase in overall network function and robustness; it contributes to the functions of other network properties (e.g. nestedness) and stability of species in a network. Increasing connectance stabilises or increases nestedness (James et al., 2012). By incorporating nestedness and connectance in a model to determine species and network persistence, James et al. (2012) showed that despite a high correlation between nestedness and connectance, when connectance was removed from the model, nestedness alone could not maintain persistence of the network. Recently, attention has been drawn to the conservation potentials of connectance, i.e. the possibility of incorporating connectance into conservation monitoring programmes (Tylianakis et al., 2010).

## 1.4: The paradox of strong contributors to network persistence and extinction vulnerability.

The theoretical basis of mutualistic interactions is challenged by the occurrence of asymmetric interactions (Bascompte et al., 2003; Vazquez & Aizen, 2004). Asymmetry implies that some species contribute more to partner wellbeing than they benefit from their partners. Unlike pair-wise interactions where cost and benefits of interacting species can be easily evaluated, contributions and benefits are often difficult to measure when individuals interact with more than one partner in a web-type structure. However, despite the difficulties associated with measuring species interaction asymmetry in multi-species systems, progress

in this direction is growing (see; Saavedra et al., 2011; Stang et al., 2006; Stang et al., 2007; Vazquez & Aizen, 2004; Vazquez et al., 2007; Vidal et al., 2014).

A paradox has emerged from investigations into the basis for asymmetric interactions in mutualistic networks (Saavedra et al. 2011). By applying a set of structural and dynamic methods (simulations) on 20 plant/insect pollinator networks, Saavedra and colleagues confirmed current theory that the removal of a strong contributor to a network tends to decrease overall network persistence more than the removal of a weak one. However, their conclusion that strong contributors to collective persistence do not gain individual survival benefits but on the contrary, are the contributors most vulnerable to extinction, is not only counter-intuitive but appears to contradict network theory. The complex simulations and purely analytical framework used by Saavedra et al. (2011), makes their conclusions very contentious. In addition, they offered no realistic or biological explanation for the outcome of their simulation experiments (James et al., 2012). To effectively understand why strong contributors are more at risk of extinction than weak ones, certain issues need to be clarified. For example:

(i) Being precise on what is measured as the unit of species strength, e.g. nestedness contribution, connectance, and contribution to reproductive fitness of interacting partners.

(ii) Evaluating how this unit or measure of strength relates to a species survival beyond analytical and statistical framework.

**1.5: Justification for research and choice of Ngel Nyaki as a study site**

There is a dearth of empirical studies, especially in Africa, of the effectiveness of visitors and the implication of strong and weak interactions for overall community persistence (Roger et al., 2004). Testing models of pollination interaction networks at Ngel Nyaki forest would not only inform and increase understanding in this part of the world, but the idea has become necessary as this forest is grouped under the tropical species-rich zone where there is an extremely scarce record of extensive mutualistic networks between plants and their pollinators (Kaiser-Bunbury et al., 2009).

Ngel Nyaki forest is recognized by BirdLife International as an Important Bird Area (IBA) (Stattersfields et al., 1998), as well as an Endemic Bird Area (EBA) and as such an ideal place to test an exclusive, sunbird-tree pollination network model. The high level of endemism of both flora and avifaunal diversity would also imply that some bipartite interactions (between sunbird species and their host tree species) would most likely be unique to this forest, necessitating a study of this nature to identify such unique interactions.

### 1.6: Aim

To use a sunbird –tree pollination network as a model system to test current network theories / hypothesis. In addition, the study will contribute towards the development of the first-ever sunbird-tree pollination web for an African montane forest.

To achieve this goal I have set out to fulfil the following objectives:

#### 1.6.1: Objectives

1. To develop a sunbird tree plant pollinator network, using flower visitation and pollen transport data.
2. Identify strong and weak contributors to the structure of the sunbird-tree

pollination network.

3. To use empirical models to estimate the level of vulnerability to extinction faced by strong contributors to network structure and persistence.
4. Determine the congruence between the flower visitation and pollen transport networks
5. Determine whether frequent flower visitors will also transport more pollen.
6. Investigate the relationship between nestedness and connectance and how they contribute to network stability and species survival.
7. Estimate two components of interaction strength between plants and pollinators; visitation frequency and pollen transportation.

**1.7: Study site:**

**1.7.1: Ngel Nyaki Forest Reserve**

The study was conducted at Ngel Nyaki Forest Reserve (07$^{o}$ 05'N 11$^{o}$ 04'E) located at the eastern edge of the Mambilla Plateau in Taraba state Nigeria (Figure 1.3) at an elevation of approximately 1550 m a.s.l (Chapman & Chapman, 2001). Ngel Nyaki Forest Reserve is 46 km$^{2}$ in extent, of which c.7.5 km$^{2}$ comprises montane/submontane forest (Chapman & Chapman, 2001). The forest is embedded within a savannah-grassland landscape of *Sporobolus* grasses as well as associated riparian forests (Chapman & Chapman, 2001; Dowsett-Lemaire, 1989).

The forest is restricted to steep, relatively inaccessible slopes that taper into perennial streams. At Ngel Nyaki, rain peaks during the months of June/July and September. Mean annual rainfall is approximately 1800 mm occurring between mid-April and mid-October (Nigerian Montane Forest Project Rainfall data). Mean maximum and minimum temperature for the wet and dry seasons are 26.1$^{o}$ C and 13.1$^{o}$C, and 23.1$^{o}$ C and 16. 1$^{o}$ C, respectively

(Mathesius et al., 2011). Daily mean temperature has never exceeded 30$^{o}$C (Ngel Nyaki weather station data).

The reserve is officially protected by the Taraba State Forest Service and the presence of NMFP researchers also has a positive influence on reducing poaching. However, local Fulani pastoralists and their cattle still remain on the reserve land, and their cows enter the forested areas, trampling and eating seedlings and compacting soil (Chapman & Chapman 2001). Additionally, the grassland is annually burnt to encourage new growth; fires encroach into the forest edge, opening it up and encouraging the growth of light demanding lianas and grasses. Outside the main Ngel Nyaki Forest, small riparian forests (Figure 1.4 c) are likewise suffering from the same fate of cattle trampling, fire encroachment, as well as the removal of poles for fence posts and fuel by the local Fulani families.

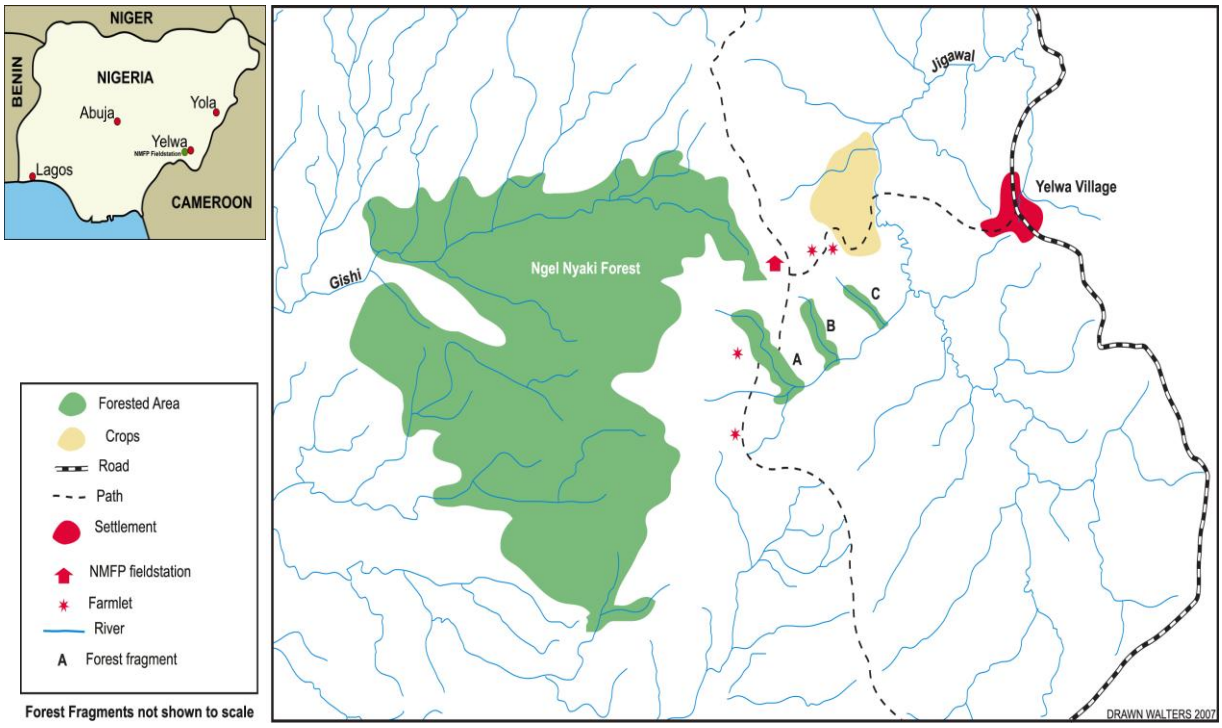



Figure 1.3: Map of Ngel Nyaki forest Reserve (left) and locator map of Ngel Nyaki (Top right).


A


B


C

Figure 1.4: Cross-sections of the Ngel Nyaki Forest Reserve. (A). Grassland tapering at the edge of core forest. (B) Inner section of the core forest. (C). Riparian fragments showing some rocky-outcrops. (Photo credit: Charles Nsor).


Figure 1.5: Map of Ngel Nyaki showing the various adjoining riparian fragments. The forest is dark green and the surrounding matrix light green/grey. The blue spot at the top corner is the spot where the map was generated using a Samsung galaxy 10.1 note GPS software.

### 1.7.2: Ngel Nyaki Flora and Fauna

Ngel Nyaki is the most floristically diverse forest of its type in Nigeria (Chapman & Chapman, 2001). Sixty nine tree species have been recorded so far, with over 146 vascular plant species collected from Ngel Nyaki, many of these being trees that are almost endemic to the Afromontane region of White (1983).

Several tree species at the time of the earliest surveys were new to West Africa, e.g. *Anthonotha noldeae*, *Apodytes dimidiate* and *Pterygota mildbraedii*; while others, such as *Isolona* cf. *deightonii*, and *Ficus chlamydocarpa*, were new to Nigeria (Dowsett-Lemaire, 1989). Five tree species are IUCN red-data listed namely; *Entandophragma angolense* (VU), *Lovoa trichiliodes* (VU), *Milletia conraui* (VU), *Pouteria altissima* (LR), *Dombeya* cf. *ledermannii* (CR) and endemic to the Cameroon Mountain range (Chapman & Chapman, 2001).

Ngel Nyaki forest is also home to several mammals and some primates, and according to Hepper (as cited in Chapman & Chapman, 2001), villagers at Ngel Nyaki were accustomed to the roar of lions, which are now locally extinct. Extant wild life at Ngel Nyaki includes; a small thriving population of the IUCN Red Data Listed Chimpanzees (*Pan troglodytes* subsp. *ellioti*), Baboons (*Papio anubis*), Putty-nose monkeys (*Cercopithecus nictitans*, subsp. martini, Black-and-white colobus (*Colobus guereza occidentalis*) and Tantalus monkeys (*Chlorocebus tantalus*) (Beck & Chapman, 2008; Chapman et al., 2004).

Other known faunal taxa include, red duiker (*Cephalophus natalensis*), civet cat (*Felis silvestris libyca*). The forest is also rich in other taxa, with many undescribed species of reptiles and amphibians (Blackburne, pers. comm.).

### 1.7.3: Important Bird Area

Birds contribute substantially to the overall species richness of the montane forests of the Cameroonian highlands, which are recognized as biodiversity hotspots of global importance (Orme et al., 2005). Ngel Nyaki forest is no exception; it is classified as a Birdlife International Important Bird Area (IBA), and is rich in endemic bird species (Stattersfields et

al., 1998). There have already been several preliminary studies into the avifauna of Ngel Nyaki forest (Hall, 1976; Ash et al., 1989; Ezealor, 2001; Osinubi et al., 2014; Nsor & Chapman, 2013; Nsor et al., 2014).

## REFERENCES


Ahmed H. M. H., Siddiq, M. A., & El-Sarrag, M. S. A. (1989). Honeybee pollination of some cultivated crops in Sudan. *Proceedings of the 4th International Conference on Apiculture in Tropical Climates, Cairo*. London International Bee Research Association, pp. 100–108.

Alarcón, R. (2010). Congruence between visitation and pollen-transport networks in a California plantâ□“pollinator community. *Oikos*, 119(1), 35-44.

Alarcón, R., Waser, N. M., & Ollerton, J. (2008). Year-to-Year Variation in the Topology of a Plant-Pollinator Interaction Network. *Oikos*, 117(12), 1796-1807.

Almeida-Neto, M., Guimaraes, P., Guimarães, P. R., Loyola, R. D., & Ulrich, W. (2008). A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos*, 117(8), 1227-1239.

Almeida-Neto, M., & Ulrich, W. (2011). A straightforward computational approach for measuring nestedness using quantitative matrices. *Environmental Modelling & Software*, 26(2), 173-178.

Ash, J., Dowsett, R., & Dowsett-Lemaire, F. (1989). New ornithological distribution records from eastern Nigeria. *Tauraco Research Report*, 1, 13-27.

Atmar, W., & Patterson, B. D. (1993). The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia*, 96(3), 373-382.

Baker, H. G., & Harris, B. J. (1957). The Pollination of Parkia by Bats and Its Attendant Evolutionary Problems. *Evolution*, 11(4), 449-460.

Baldock, K. C. R., Memmott, J., Ruiz-Guajardo, J. C., Roze, D., & Stone, G. N. (2011). Daily temporal structure in African savanna flower visitation networks and consequences for network sampling. *Ecology*, 92(3), 687-698.

Bascompte, J., & Jordano, P. (2007). Plant-animal mutualistic networks: the architecture of biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 567-593.

Bascompte, J., Jordano, P., Melián, C. J., & Olesen, J. M. (2003). The Nested Assembly of Plant-Animal Mutualistic Networks. *Proceedings of the National Academy of Sciences of the United States of America*, 100(16), 9383-9387.

Bastolla, U., Fortuna, M. A., Pascual-Garcia, A., Ferrera, A., Luque, B., & Bascompte, J. (2009). The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature*, 458(7241), 1018-1020.

Beck, J., & Chapman, H. M. (2008). A population estimate of the endangered chimpanzee Pan troglodytes vellerosus in a Nigerian montane forest: implications for conservation. *Oryx*, 42(03), 448-451.

Berlow, E. L. (1999). Strong effects of weak interactions in ecological communities. *Nature*, 398(6725), 330-334.

Berlow, E. L., Navarrete, S. A., Briggs, C. J., Power, M. E., & Menge, B. A. (1999). Quantifying variation in the strengths of species interactions. *Ecology*, 80(7), 2206-2224.

Berlow, E. L., Neutel, A., Cohen, J. E., DeRuiter, P. C., Ebenman, B. O., Emmerson, M., . . . Kokkoris, G. D. (2004). Interaction strengths in food webs: issues and opportunities. *Journal of animal ecology*, 73(3), 585-598.

Bronstein, J., & McKey, D. (1989). The fig/pollinator mutualism: a model system for comparative biology. *Cellular and Molecular Life Sciences*, 45(7), 601-604.

Bronstein, J. L. (1994). Our current understanding of mutualism. *Quarterly Review of Biology*, 31-51.

Bronstein, J. L. (2001). The Costs of Mutualism. *American Zoologist*, 41(4), 825-839.

Bronstein, J. L., Wilson, W. G., & Morris, W. F. (2003). Ecological dynamics of mutualist/antagonist communities. *The American Naturalist*, 162(S4), S24-S39.

Brualdi, R. A., & Sanderson, J. G. (1999). Nested species subsets, gaps, and discrepancy. *Oecologia*, 119(2), 256-264.

Carvalheiro, L. G., Veldtman, R., Shenkute, A. G., Tesfay, G. B., Pirk, C. W., Donaldson, J. S., & Nicolson, S. W. (2011). Natural and within-farmland biodiversity enhances crop productivity. *Ecology Letters*, 14(3), 251-259.

Chapman, J. D., & Chapman, H. M. (2001) *The Forests of Taraba and Adamawa States, Nigeria. An Ecological Account and Plant Species Checklist*. University of Canterbury, Christchurch, New Zealand.

Chapman, H. M., Olson, S. M., & Trumm, D. (2004). An assessment of changes in the montane forests of Taraba State, Nigeria, over the past 30 years. *Oryx*, 38(3), 282-290.

Connor, R. C. (1996). Partner preferences in by-product mutualisms and the case of predator inspection in fish. *Animal Behaviour*, 51(2), 451-454.

Doebeli, M., & Knowlton, N. (1998). The evolution of interspecific mutualisms. *Proceedings of the National Academy of Sciences*, 95(15), 8676-8680.

Dowsett-Lemaire, F. (1989). The flora and phytogeography of the evergreen forests of Malawi I: Afromontane and mid-altitude forests. *Bulletin du Jardin botanique national de Belgique/Bulletin van de Nationale Plantentuin van Belgie*, 3-131.

Ezealor, A. (2001). Nigeria: Important Bird Areas in Africa and Associated Islands: priority sites for Conservation. *BirdLife Conservation series*(11), 673-682.

Fukui, S., & Yamauchi, A. (2011). Evolution of situation-dependent mutualism. Journal *of Plant Interactions*, 6(2-3), 179-180.

Hall, P. (1976). The birds of Mambilla Plateau. *Bulletin of the Nigerian Ornithological Society*, **12**, 67-72.

Holland, J. N., Chamberlain, S. A., & Miller, T. E. (2011). Consequences of ants and extrafloral nectar for a pollinating seed-consuming mutualism: ant satiation, floral distraction or plant defense? *Oikos*, 120(3), 381-388.

James, A., Pitchford, J. W., & Plank, M. J. (2012). Disentangling nestedness from models of ecological complexity. *Nature*, 487(7406), 227-230.

Kaiser-Bunbury, C. N., Memmott, J., & Müller, C. B. (2009). Community structure of pollination webs of Mauritian heathland habitats. *Perspectives in Plant Ecology, Evolution and Systematics*, 11(4), 241-254.

Knowlton, N., & Rohwer, F. (2003). Multispecies microbial mutualisms on coral reefs: the host as a habitat. *The American Naturalist*, 162(S4), S51-S62.

Lawton, J. (1978). Host-plant influences on insect diversity: the effects of space and time. *Diversity of Insect Faunas*: 105-125.

Lopezaraiza–Mikel, M. E., Hayes, R. B., Whalley, M. R., & Memmott, J. (2007). The impact of an alien plant on a native plant–pollinator network: an experimental approach. *Ecology Letters*, 10(7), 539-550.

Matthesius, A., Chapman, H., & Kelly, D. (2011). Testing for Janzen–Connell effects in a West African montane forest. *Biotropica*, 43(1), 77-83.

May, R. M. (1972). Will a Large Complex System be Stable? *Nature*, 238(5364), 413- 414.

McCann, K. S. (2000). The diversity–stability debate. *Nature*, 405(6783), 228-233.

Memmott, J. (1999). The structure of a plant-pollinator food web. *Ecology Letters*, 2(5), 276-280.

Memmott, J., Waser, N. M., & Price, M. V. (2004). Tolerance of Pollination Networks to Species Extinctions. *Proceedings: Biological Sciences*, 271(1557), 2605-2611.

Montoya, J. M., Pimm, S. L., & Solé, R. V. (2006). Ecological networks and their fragility. *Nature*, 442(7100), 259-264.

Montoya, J. M., & Solé, R. V. (2002). Small world patterns in food webs. *Journal of theoretical biology*, 214(3), 405-412.

Nielsen, A., & Bascompte, J. (2007). Ecological networks, nestedness and sampling effort. *Journal of Ecology*, 95(5), 1134-1141.

Nsor, C. A., & Chapman, H. M. (2013). A preliminary investigation into the avian pollinators of three tree species in a Nigerian Montane Forest. *Malimbus*, 35, 37-49.

Nsor, C. A., Nicodemus, E., & Bashiru, U. (2014). First record of Bamenda Apalis *Apalis bamendae* for Nigeria. *Bulletin of African Bird Club* (Vol 21), No 1.

Orme, C.D.L., Davies, R. G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V. A., . . . Ridgely, R. S. (2005). Global hotspots of species richness are not congruent with endemism or threat. *Nature*, 436(7053), 1016-1019.

Osinubi, S. T., Vugeh, Y., Briskie, J. V., Ottosson, U., Brown, J. A., & Chapman, H. M. (2014). Association with riparian fragments by Yellow-breasted Boubou atroflavus indicates need for wider-scale forest matrix conservation. *Malimbus* 36(1), 47-57.

Palmer, T. M., Stanton, M. L., & Young, T. P. (2003). Competition and coexistence: exploring mechanisms that restrict and maintain diversity within mutualist guilds. *The American Naturalist*, 162(S4), S63-S79.

Patterson, B. D., & Atmar, W. (1986). Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biological Journal of the Linnean Society*, 28(1-2), 65-82.

Petanidou, T., & Potts, S. G. (2006). Mutual use of resources in Mediterranean plant–pollinator communities: how specialised are pollination webs. *Plant–pollinator interactions*: from specialisation to generalisation, 220-244.

Price, P. W., Bouton, C. E., Gross, P., McPheron, B. A., Thompson, J. N., & Weis, A. E. (1980). Interactions among three trophic levels: influence of plants on interactions

between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics*, 41-65.

Rezende, E. L., Jordano, P., & Bascompte, J. (2007). Effects of phenotypic complementarity and phylogeny on the nested structure of mutualistic networks. *Oikos*, 116(11), 1919-1929.

Rogers, J. G., Balkwill, K., & Gemmill, B. (2004). African pollination studies: where are the gaps? *International Journal of Tropical Insect Science*. 24, 5-28.

Saavedra, S., Stouffer, D. B., Uzzi, B., & Bascompte, J. (2011). Strong contributors to network persistence are the most vulnerable to extinction. *Nature*, 478(7368), 233.

Stachowicz, J. J. (2001). Mutualism, Facilitation, and the Structure of Ecological Communities. *Bioscience*, 51(3), 235-246.

Stang, M., Klinkhamer, P. G., & Van Der Meijden, E. (2006). Size constraints and flower abundance determine the number of interactions in a plant–flower visitor web. *Oikos*, 112(1), 111-121.

Stang, M., Klinkhamer, P. G., & van der Meijden, E. (2007). Asymmetric specialisation and extinction risk in plant-flower visitor webs: a matter of morphology or abundance? *Oecologia*, 151(3), 442-453.

Staniczenko, P. P. A., Kopp, J. C., & Allesina, S. (2013). The ghost of nestedness in ecological networks. *Nature communications*, 4, 1391.

Stanton, M. L. (2003). Interacting Guilds: Moving beyond the Pairwise Perspective on Mutualisms. *The American Naturalist*, 162(S4), S10-S23.

Stattersfield, A., Crosby, M., Long, A., & Wege, D. (1998). *Endemic Bird Areas of the World*: priorities for biodiversity conservation, BirdLife International, Cambridge, UK.

Thomson, J. (2003). When is it mutualism? *The American Naturalist*, 162(S4), S1-S9.

Tscharntke, T., Bommarco, R., Clough, Y., Crist, T. O., Kleijn, D., Rand, T. A., . . . Vidal, S. (2007). Conservation biological control and enemy diversity on a landscape scale. *Biological Control*, 43(3), 294-309.

Tylianakis, J. M., Tscharntke, T., & Lewis, O. T. (2007). Habitat modification alters the structure of tropical host–parasitoid food webs. *Nature*, 445(7124), 202-205.

Tylianakis, J. M., Laliberté, E., Nielsen, A., & Bascompte, J. (2010). Conservation of species interaction networks. *Biological Conservation*, 143(10), 2270-2279.

Ulrich, W. (2009). Ecological interaction networks: prospects and pitfalls. *Ecological Questions*, 11(1), 17-25.

Ulrich, W., & Almeida-Neto, M. (2012). On the meanings of nestedness: back to the basics. *Ecography* (Cop.), 35(10), 865-871.

Vázquez, D. P., & Aizen, M. A. (2004). Asymmetric specialisation: a pervasive feature of plant-pollinator interactions. *Ecology*, 85(5), 1251-1257.

Vázquez, D. P., Blüthgen, N., Cagnolo, L., & Chacoff, N. P. (2009). Uniting pattern and process in plant-animal mutualistic networks: a review. Oxford University Press, England, pp. 1445-1457.

Vázquez, D. P., Lomascolo, S. B., Maldonado, M. B., Chacoff, N. P., Dorado, J., Stevani, E.L., & Vitale, N. L. (2012). The strength of plant-pollinator interactions. *Ecology*, 93(4), 719-725.

Vazquez, D. P., Melian, C. J., Williams, N. M., Bluthgen, N., Krasnov, B. R., & Poulin, R. (2007). Species abundance and asymmetric interaction strength in ecological networks. *Oikos*, 116(7), 1120-1127.

Vidal, M. M., Hasui, E., Pizo, M. A., Tamashiro, J. Y., Silva, W. R., & Guimaraes Jr., P. R. (2014). Frugivores at higher risk of extinction are the key elements of a mutualistic network. *Ecology*.

Waser, N. M. (1987). Spatial genetic heterogeneity in a population of the montane perennial plant Delphinium nelsonii. *Heredity* (Edinb), 58(2), 249-256.

White, F. (1983). *The Vegetation of Africa*. UNESCO, Paris,France.

Wootton, J. T., & Emmerson, M. (2005). Measurement of interaction strength in nature. *Annual Review of Ecology, Evolution, and Systematics*, 419-444.

Wright, D. H., & Reeves, J. H. (1992). On the meaning and measurement of nestedness of species assemblages. *Oecologia*, 92(3), 416-428.

Zavaleta, E. S., Hobbs, R. J., & Mooney, H. A. (2001). Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology & Evolution*, 16(8), 454-459.

## CHAPTER TWO

**How do changing landscapes and fragmented habitats affect sunbird distribution and abundance at Ngel Nyaki forest reserve?**

## ABSTRACT

The conversion of habitats through anthropogenic disturbance leads to habitat fragmentation; a common threat to biodiversity across diverse ecosystems. Habitat fragmentation is the primary cause of bird species loss and decrease in the abundance of surviving species. Given the rising demand for agricultural land as a result of increasing human population, managing fragmented and human modified habitats to sustainably support the needs of people while still sustaining biodiversity is crucial.

In this chapter, I examined the effect of habitat structure on the abundance and diversity of sunbird species in a fragmented Afro-montane forest landscape. I compared the abundance, species richness and diversity of sunbird species between islands of small, degraded, riparian fragments in overgrazed grassland and in edge habitat of a nearby protected continuous forest (main forest), in order to determine if the forest fragments are as suitable a habitat to sunbirds as the edge of the main forest. The latter is known to be optimal sunbird habitat. Eleven sunbird species from four genera accounted for a total of 1,432 individuals observed. Ten species were found in the edge of the main forest. The main forest was richer in species (three unique species) than the fragments. However, there was no significant difference in species abundance between the two habitats. Sunbird species from the genus *Cinnyris* were the most abundant. I recorded a new record for the Mambilla plateau, *Anthreptes rectirostris*, which suggests that the avian diversity of Ngel Nyaki may be underexplored. Another, notable finding was the record for the first time in Nigeria of Bamenda Apalis *Apalis bamendae*, a

species previously considered to be endemic to the Bamenda highlands of Cameroon. Although our results suggest that fragmentation is not yet a threat to sunbird distribution in the reserve, anthropogenic disturbance such as the annual burning of grassland may alter crucial habitats for sunbird survival.

## 2.0: Introduction

Habitat conversion through anthropogenic disturbance is the foremost global cause of species loss and decrease in abundance of surviving species. It is a common threat to biodiversity across a diversity of tropical and temperate ecosystems (Foley et al., 2005). Tropical deforestation represents the greatest threat to world's biodiversity since tropical forests support about 70 % of the earth's flora and fauna (Noss, 1991).

Habitat fragmentation has been identified as the primary cause of bird species loss (Wilcove et al., 1986). Recent assessments of the world's birds revealed that about 1,308 species (13 % of extant species) are globally threatened with extinction (BirdLife International, 2013). In Nigeria, the focus of this study, 19 of about 910 (2%) extant bird species are currently facing extinction threats (IUCN Red List, 2012). The loss of diversity is enhanced by the uneven patterns of distribution of species, especially with most threatened species disproportionately concentrated in small and highly threatened areas (Purvis & Hector, 2000; Sechrest et al., 2002). For instance, about 44 % of vascular plants and 35 % of vertebrates are endemic to 25 biodiversity hotspots occupying 1.4 % of the planet's land (Myers et al., 2000). Regrettably, people and therefore threats to biodiversity follow the same pattern of distribution (Sechrest et al., 2002). Human presence and the pressure they impose on these global size-constrained biodiversity hotspots results in loss of phenotypic and genetic diversity through population

decline, despite the seeming persistence of species. This is worrying because we stand to lose the unique evolutionary history of most species that are endemic to these biodiversity hot-spots around the world (Sechrest et al., 2002).

Africa is among the world's major centres of endemism, evolutionary uniqueness, and biodiversity (Klein et al., 2007; Purvis et al., 2000) yet loss of population and genetic diversity is more extreme in Africa than anywhere else. Klein et al. (2007), attributes this high level of vulnerability to Africa's high human population and the pressure this rising population imposes on available land and forest. Managing fragmented and human modified habitats to sustainably support the needs of people while still sustaining biodiversity is a major challenge. However, some species can persist in fragmented or modified habitats for a long while. Thus, studies to identify species that are perhaps vulnerable or species that can cope in disturbed habitats are necessary to guide conservation actions. In addition, periodic population level assessments of indicator species such as birds could lead to timely detection of threats or pressures faced by various species. These threatened species are usually identified by carrying out censuses to determine whether populations are stable, in decline or on the rise.

### 2.1: Birds as indicators of degraded habitats

Birds are among the most mobile organisms on earth, with a widespread occurrence in most habitats, especially terrestrial ones (Padoa-Schioppa et al., 2006) which makes them useful indicators of environmental health (Gregory et al., 2003; Pearce & Ferrier, 2001). Furthermore, with the exception of the Cape floristic region of South Africa, studies have shown that most centres of high bird endemism are also good indicators for other terrestrial biodiversity, as it has been established that most centres of endemism are usually very rich in

species diversity (Norris & Pain, 2002; McKay & Coulthard, 2000). Thus, centres of bird endemism are good starting points for setting conservation priorities on a broad scale.

Their conspicuousness, high sensitivity to environmental changes, and relative low number of species(10,000 globally compared to about 300,000 plant species or over 900,000 insect species (IUCN, 2012)), makes birds very suitable for ecological monitoring studies. Bird's sensitivity to environmental change is a vital feature for assessing environmental health. This sensitivity is displayed in several ways, for example through habitat selection, seasonal migration and the synchronisation of life history processes such as breeding to coincide with seasonal availability of resources (Durant et al., 2007; Thomas et al., 2001). This strong association between birds and the environment has been explored over the years by ecologists to tackle vital ecological issues such as climate change (Furness & Greenwood, 1993; Gregory et al., 2009), habitat degradation/fragmentation (Abalaka et al., 2007; Pauw & Louw, 2012; Pearce & Ferrier, 2001; Usieta et al., 2013), land use policies (Atauri & de Lucio, 2001; Hinsley & Bellamy, 2000), and for setting conservation priority (Norris & Pain, 2002; Dami et al., 2014). It is therefore essential to constantly monitor bird abundance and diversity to see how birds cope in environments that are constantly changing as a result of disturbance through human induced alterations of habitats.

## 2.2: Spatial abundance and distribution of birds: the implication for ecosystem processes and functions.

A long standing goal of community ecology is to find patterns in species assembly (Diamond & Case, 1986). This is crucial because, by identifying patterns, we can formulate hypotheses about the processes that generate these patterns. But despite growing emphasis on the relevance of species spatial patterns, the consequences for ecosystem functioning and processes, for example pollination, remain poorly understood, probably because few studies

have empirically evaluated the relationship between such patterns and most ecosystem processes (Kikvidze et al., 2005; Maestre et al., 2005; Pringle et al., 2010). However, there is growing improvement. For example, Pringle et al. (2010) showed that the regular, even-spaced spatial patterns of termite mounds found in a homogeneous African savannah provided a guide for parallel spatial patterning in tree-dwelling, termite-dependent animal communities. Their findings that the uniformity of these patterns at small spatial scales enhanced productivity of the whole landscape provide support for models linking spatial patterns with ecosystem processes and functioning (Memmott et al., 2004; Rietkerk et al., 2004). The above finding also holds for other cooperative systems such as plant-pollinator interactions (Vázquez et al., 2009); where abundance is known to positively affect pollination (Vázquez et al., 2012; Vazquez et al., 2007; Vázquez et al., 2005). This is based on the premise that the more abundant a species is, the more likely it is to be visited by common and even rare species, hence maximising its fitness.

In this study, I examined the effect of landscape structure on the spatial abundance and diversity of sunbird species in a fragmented Afro-montane forest landscape. The aim of this study was to assess how well human modified landscapes are able to support sunbird abundance and diversity. The results of the study will serve as a guide towards the management of disturbed habitats and a template for the protection of other forms of biodiversity and the network of cooperation and facilitation – e.g. pollination.

Using this approach, I addressed the following goals to:

i). Develop a comprehensive check-list of sunbird species at Ngel Nyaki forest.

ii). Determine whether species richness/abundance differs between two habitat types – riparian forest fragments and the edge of continuous forest.

iii) Identify rare and abundant species of sunbirds at Ngel Nyaki

I tested the hypothesis:

As habitat quality and size has no effect on abundance and diversity, there will be no difference in abundance and diversity of sunbird species between the two habitat types.

## 2.3: Study Site

### 2.3.1: Ngel Nyaki Forest Reserve

The study was conducted at Ngel Nyaki Forest Reserve ($07^{o}$ 05'N $11^{o}$ 04'E) located at the eastern edge of the Mambilla Plateau in Taraba state Nigeria (Figure 1.3, chapter 1) at an elevation of approximately 1550 m a.s.l (Chapman & Chapman, 2001). Ngel Nyaki Forest Reserve is 46 $km^2$ in extent, of which c.7.5 $km^2$ comprises montane/submontane forest (Chapman & Chapman, 2001). The forest is embedded within a savannah-grassland landscape of *Sporobolus* grasses as well as associated riparian forests (Chapman & Chapman, 2001; Dowsett-Lemaire, 1989).

The forest is restricted to steep, relatively inaccessible slopes that taper into perennial streams. At Ngel Nyaki, rain peaks during the months of June/July and September. Mean annual rainfall is approximately 1800 mm occurring between mid-April and mid-October (Nigerian Montane Forest Project Rainfall data). Mean maximum and minimum temperature for the wet and dry seasons are $26.1^{o}$ C and $13.1^{o}$C, and $23.1^{o}$ C and 16. $1^{o}$ C, respectively (Mathesius et al., 2011

### 2.3.2: Ecological/conservation status and relevance of Ngel Nyaki forest reserve

Ngel Nyaki forest, like much of the Cameroon Mountains, is a Birdlife International IBA (Important Bird Area), and rich in endemic bird species (Stattersfield et al., 1998). Birds

contribute substantially to the overall species richness of West African forests, currently recognized as biodiversity hotspots of global importance (Orme et al., 2005).

Although very little literature existed (Ash et al., 1989) on the rich avifauna of this region, the establishment of the Nigerian montane forest project (NMFP), about a decade ago, has remarkably boosted research interest in the faunal diversity of Ngel Nyaki forest (NMFP annual report, 2012, 2013). In addition, the high species richness and endemism of birds in Ngel Nyaki forest reported by some of the earliest surveys (Hall, 1976) has recently attracted more ornithological research (Ezealor, 2001; Weston et al., 2012; Nsor & Chapman, 2013; Nsor et al., 2014; Osinubi et al., 2014). However, none of this research has focused on detailed assessment of the distribution and diversity of specific taxon, or specifically investigated the diversity and abundance of sunbird species (Nectariniidae).

### 2.3.3: Threats and challenges to Ngel Nyaki forest stability and species diversity

Despite official protection since 1969, Ngel Nyaki forest is threatened by increasing demand for arable land for subsistence agriculture due to increasing human population. Immediate threats include trampling by cattle, bush meat hunting, over-grazing by Fulani cattle herders and the annual indiscriminate burning of grassland and savannah to stimulate new growth of grasses for cattle grazing, especially along the forest edge.

However, the forest structure and composition have persisted and some of the forest within the reserve is relatively undisturbed due to the steep, relatively inaccessible slopes and the superstitious believes/local taboos of the Yelwa people, especially their awe-stricken customary reverence of mountains (Chapman & Chapman, 2001). These traditional views and customs for example, forbidding the eating of primates, have helped considerably, and

accounts for the comparatively high diversity that is still found in this forest in contrast to other nearby lowland forests.

## 2.4: Study Species

Sunbirds are among the most common bird species encountered daily at Ngel Nyaki forest (Nsor unpublished data). They are small passerine birds (members of the large order Passeriformes), often referred to as “perching birds” or “song birds." They belong to the family Nectariniidae (Mann & Cheke, 2010).

Sunbirds account for about 68.2 % of the 176 notable species in the Nectariniidae family. With a total of 120 known species in 15 genera, sunbirds are undoubtedly the most dominant in the Nectariniidae family. Of the 120 known species of sunbirds in the world, 88 species in 11 genera occur in Africa, 33 in the West African sub-region; while, 27 occur in Nigeria (Mann & Cheke, 2010).

Sunbirds are strongly sexually dimorphic, with the males usually brilliantly plumaged in iridescent colours (Mann & Cheke, 2010). In addition, the tails of many species are longer in males; overall males are larger. Sunbirds are quite distinct from other bird species. They are active, restless and can be easily identified by their unique and peculiar features, which include their long, slender, pointed, or decurved bills, with tubular tongues (Figure 2.1). Both bill shape and tongue are unique adaptation to their nectar feeding habit (Mann & Cheke, 2010).

Figure 2.1: A common sunbird species (variable sunbird *C. venustus*) at the study site, illustrating the decurved beak and irridescent plumage. Relative size (10 cm),Photo credit: Charles Nsor.

## 2.5: Methodology

### 2.5.1: Line Transects

Line transect census technique was used to estimate diversity and abundance of sunbird species (Bibby et al., 2001). Sampling was carried out between 6:30 am - 9:30 am and between 3:30 pm -6:30 pm each day. The survey took place between November, 2012 to February, 2013 and later between November, 2013 and February, 2014. A total of 19 transects ranging between 336 m to 1,737 m in length and covering a total distance of 16,654 m or 16.7 km were surveyed. Transects were selected with a view to obtain a representative data that would account for the diversity of sunbird species at Ngel Nyaki forest reserve. eleven transects were laid along the edges of the core forest on the eastern side of the reserve,

two in the openings within the core, while the other six were scattered within riparian fragments (Figure 2.2). Each transect was surveyed twice from November 2012 to February 2013 and November 2013 to February 2014, making a total of four sessions per transect (morning and evening).

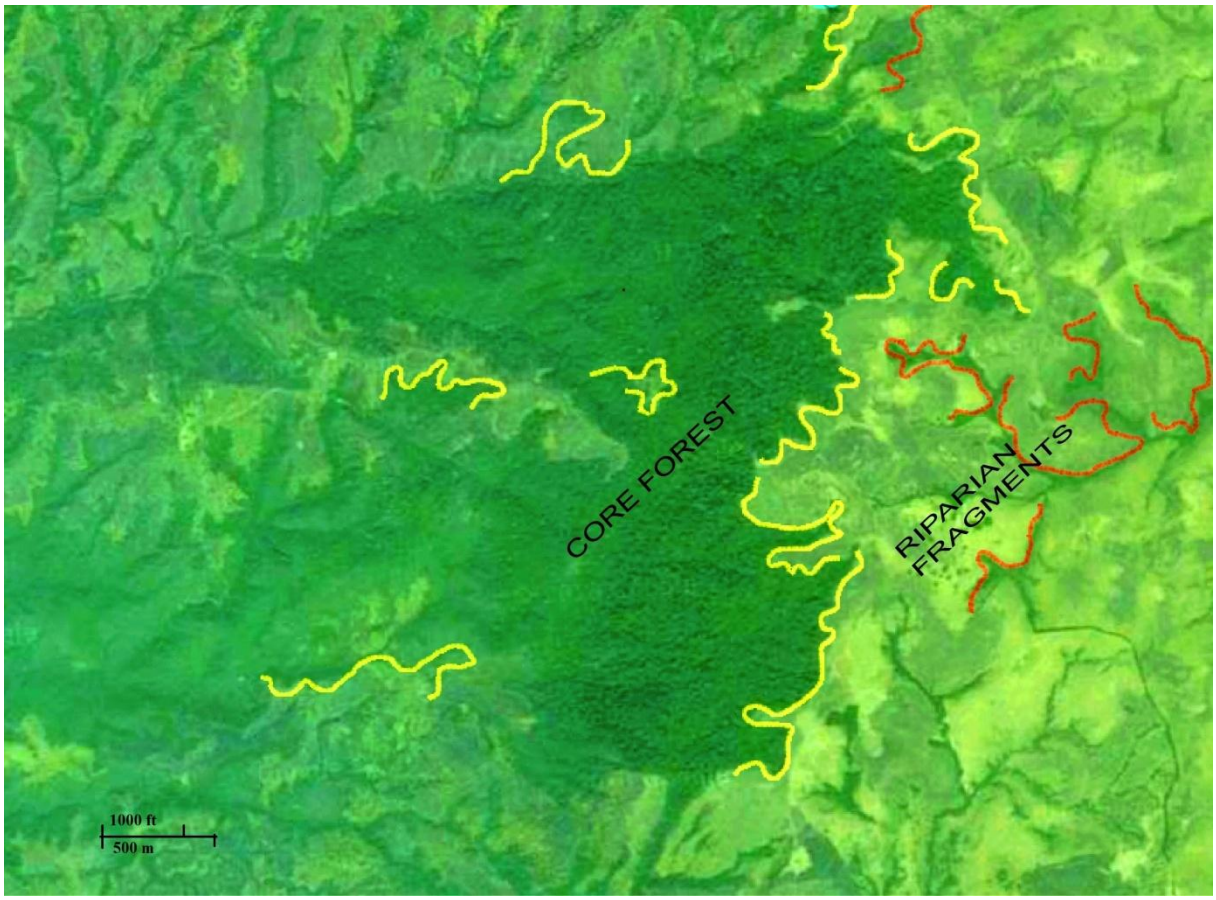



Figure.2.2: Map showing layout of transects used during sunbird species abundance and diversity survey at Ngel Nyaki forest (map was generated using GPS supported map application software on Samsung galaxy note 10.1'). Yellow outlines represent transects placed along the edge of continuous forest, while red represents transects in the riparian forest fragments. Deep green area is the continuous forest while strips of green are the surrounding riparian fragments. The grey/brown surface represents grassland.

During each observation session, my field assistant and I walked slowly along each transect, recording birds seen to at least 50 m on either side of the transects. Whenever a bird was sighted, the total distance away from the point of origin and approximate coordinates were recorded using a Garmin GPS etrex 10. A pair of Nikon binoculars (9 x 40) was used to confirm the identity of birds located by eye. Only birds visually identified were included in the census data, as it was difficult to estimate the actual number of individuals based on calls alone. Other parameters recorded during transect monitoring sessions included: i) time an individual sunbird species was sighted, ii) the number of individuals sighted, iii) the species identity and iv) the closest flowering tree species (within a radius of approximately 20 m) to the location of the bird species at the time of sighting. Additional information on species diversity was obtained from mist-netting conducted at various locations across the forest (Figure 2.3). Mist nets were set up and monitored in the morning 6:00 am to 10:00, and evening at 3:30 pm to 5:30 pm (see details in chapter three). In addition, I included two species that were only observed during flower visitation at a separate time since the objective was to identify all sunbird species in the reserve (methods, chapter three).

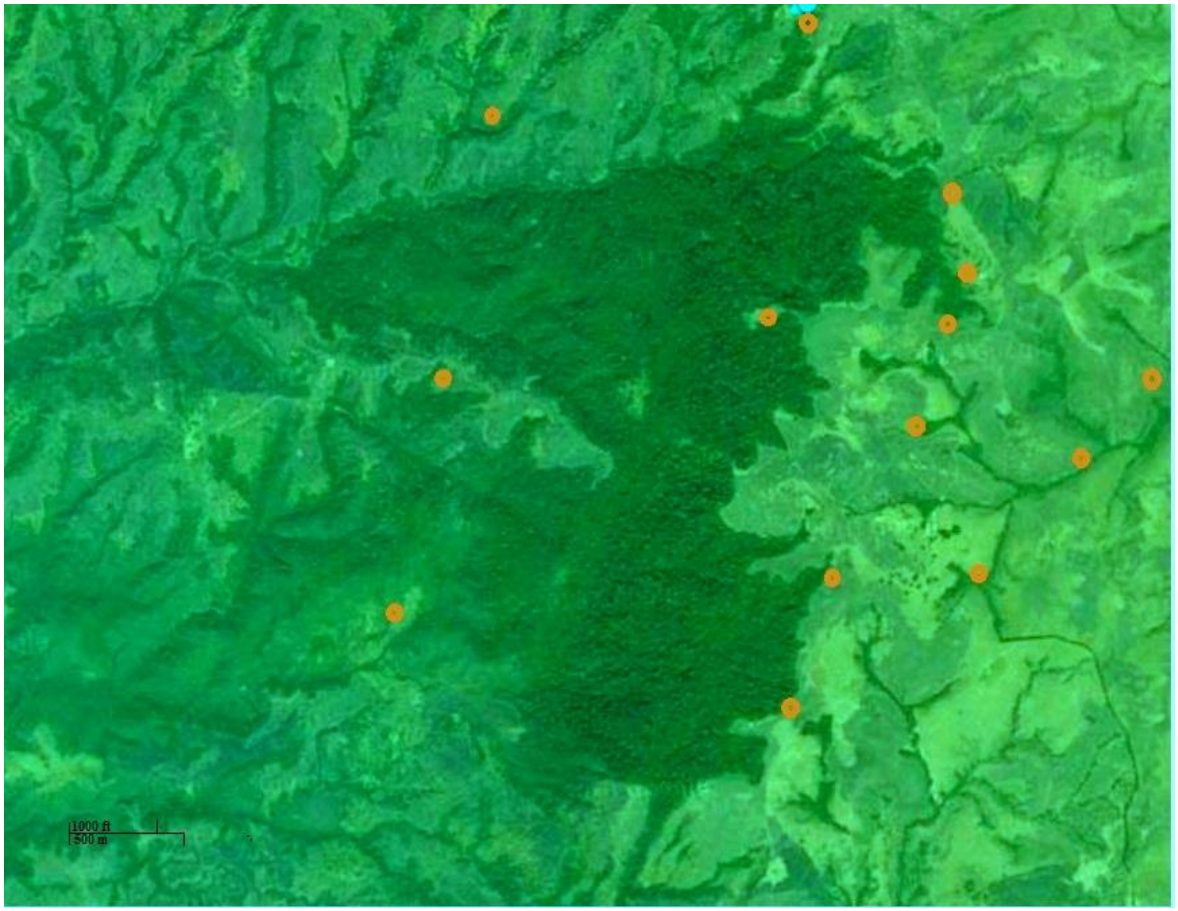


Figure 2.3: Map showing the various locations were bird-trapping (mist-netting) was conducted at Ngel Nyaki. The big deep-green area represents the continuous forest, the strips of green represents riparian fragments. Orange coloured dots are the various locations where mist-netting was carried out.

## 2.6: DATA ANALYSIS

### 2.6.1: Sunbird Diversity

In order to estimate the diversity of sunbird species in each habitat it is necessary to calculate the two components of diversity: i) number of species and ii) the relative abundance of these species i.e. their evenness). Several different indices of biodiversity are commonly used in ecological studies and I chose a common one, the Shannon Wiener Diversity index $H'$.

H' is a measure of uncertainty in predicting the species identity of an individual that is taken at random from the data set.

H' is not a measure of true diversity. True diversity, the *effective number of species* (Jost, 2006) is the number of equally-common species required to give a particular value of an index), and requires further mathematical exploration to derive the true diversity, (see equations 2.1 and 2.2 below and Table 2.1). To determine Shannon Weiner species diversity, the proportion of species (i) relative to the total number of species (pi) is calculated, and then multiplied by the natural logarithm of this proportion (lnpi), see equation 2.1 below.

$$\text{Shannon Weiner index H'} = -\sum_{i=1}^{S} p_i log_e p_i \qquad \text{Equation 2.1}$$

$$\text{H'(Shannon Weiner index)} = -p_i log_e p_i$$

Where pi = the proportion of individuals of species "i" in relation to the total population of all species.

H' = Shannon Wiener Diversity Index. $\log_e$ = natural logarithm of base e

To get the *effective number of species*, (the true value of diversity), I used the equation:

$$\exp\ (\text{H'})\ or\ \exp\ (-\sum_{i=1}^{s} p_i log_e p_i) \qquad \text{Equation 2.2}$$

A measure of true diversity of the different habitats makes it feasible to compare them. For example in a hypothetical community with equal number of individuals of each species (Table 2.1), and a species count of 5, species richness (true diversity) = 5.

Table 2.1: Hypothetical distribution of species and the procedure for calculating Shannon Wiener Diversity index and effective number of species (true diversity).

| Species | No. Of individuals | pi | lnpi | pi(lnpi) | | |
|---|---|---|---|---|---|---|
| A | 1 | 0.2 | -1.60944 | -0.32189 | | |
| B | 1 | 0.2 | -1.60944 | -0.32189 | | |
| C | 1 | 0.2 | -1.60944 | -0.32189 | | |
| D | 1 | 0.2 | -1.60944 | -0.32189 | | |
| E | 1 | 0.2 | -1.60944 | -0.32189 | | |
| Total | 5 | | H' | -1.60944 | 1.609 | |
| | | Effective number of species= | | | 4.997811 | 5 |

Using equation 2.2 below:

$$H' - \sum_{i=1}^{s} p_i log_e p_i$$

The Shannon Wiener diversity index = 1.609. I then used this exponent of this value (H') to calculate the *effective number of species*, which is the real diversity. Exp (1.609) = 5 (Jost, 2006).

I estimated species richness as counts of the various species found in the two habitats, and species evenness as a measure of biodiversity, which quantifies how equal species in a community are numerically (Mulder et al., 2004). This was determined by comparing the effective number of species to the species richness.

Two functional habitat groups were identified in this study: edge of core forest (yellow) here after referred to as main forest and riparian fragments (red) (Figure 2.2). Independent sample T-test was used to compare the abundance of species between the two habitat classes.

I used the Jaccard similarity index to estimate the difference in species diversity (species composition) between the two habitat types. Jaccard index compares the similarity and diversity of sample sets, and is the value obtained when the size of the intersection is divided by the size of the union of two sample sets (in this case the species composition in two habitats).

I used the equation:

$$C_j = \frac{a}{(a+b+c)}$$ Equation 2.3

Where $C_J$ = Jaccard index or coefficient of similarity, $a$ = number of species found in both habitats. b and $c$ are two sample sets (habitats); $b$ represents number of species found in sample $b$ and not $c$ (i.e. species unique to $b$), while $c$ represents number of species found in $c$ and not in $b$ (i.e. species unique to $c$). Jaccard similarity index ranges from 0 when no species are shared or common to both habitats, to 1 when the species compositions are identical.

To account for unequal sample sizes (i.e. unequal number of transects in this case) between habitats (main forest and fragments), I used sample-based rarefaction curves to estimate species richness, with the site as the sample unit (Gotelli & Colwell 2001). Rarefaction tests ensure that the difference in species diversity between habitats is not simply a function of sample size.

The vegan package in R was used for the rarefaction analysis. All other analyses were done using IBM SPSS version 21.0 (IBM Corp, 2012).

## 2.7: Results

### 2.7.1: Variation in sunbird species distribution and abundance with habitat

Eleven species of sunbirds accounted for a total of 1,432 individuals sighted and recorded during the survey.

There were more species in the main forest than in the fragment (ten of eleven species in the main forest and seven of eleven in the fragment) (Table 2.2). However, I found no significant difference in mean abundance (number of individuals) between main forest habitat (75.3/obs. hr, SD = 112.86) and fragment (97.0, SD = 103.77), ($t = -0.40$, $DF = 15$, $p = 0.69$) (Fig 2.4 and Table 2.2).

**Species richness and Shannon Wiener diversity**

My results demonstrate that the main forest (edge) was more species rich than the fragments; (main forest = 10, and fragment = 7). This difference in species richness is reflected in the Shannon Weiner Index: (H' for core forest = 0.65 (with an effective species count of 1.92) and H' for Fragment = 0.6, effective species count of 1.82). Overall sunbird diversity for Ngel Nyaki Forest H' = 0.65(1.92 effective number of species). The results of rarefaction test (main forest or edge = 9.9, and fragment = 7) corresponds with the species richness result above (main forest = 10, and fragment = 7). This result indicates that species richness is not a function of the sample size in this study (i.e. more transects in main forest than fragment).

**NOTE:** For a community with even species frequencies or relative abundance (pi), the effective number of species is always equal to the species richness of the community (see Table 2.1). But this is never the case in nature; thus, the effective number of species derived from the Shannon Wiener index is always less that the true diversity (species richness). This indicates the degree of dominance or variation (species evenness) in terms of relative

abundance of species in each habitat (Jost, 2006). The closer the value (effective number of species) is to species richness, the lesser the variation in relative abundance of species and vice versa. From our results, we see that, there is uneven distribution of species across habitats. There is relatively less variation in abundance in fragments (1.82: 7 species) than in the core (1.92: 10 species). This variations increases even more for the entire forest reserve (1.92: 11 species).

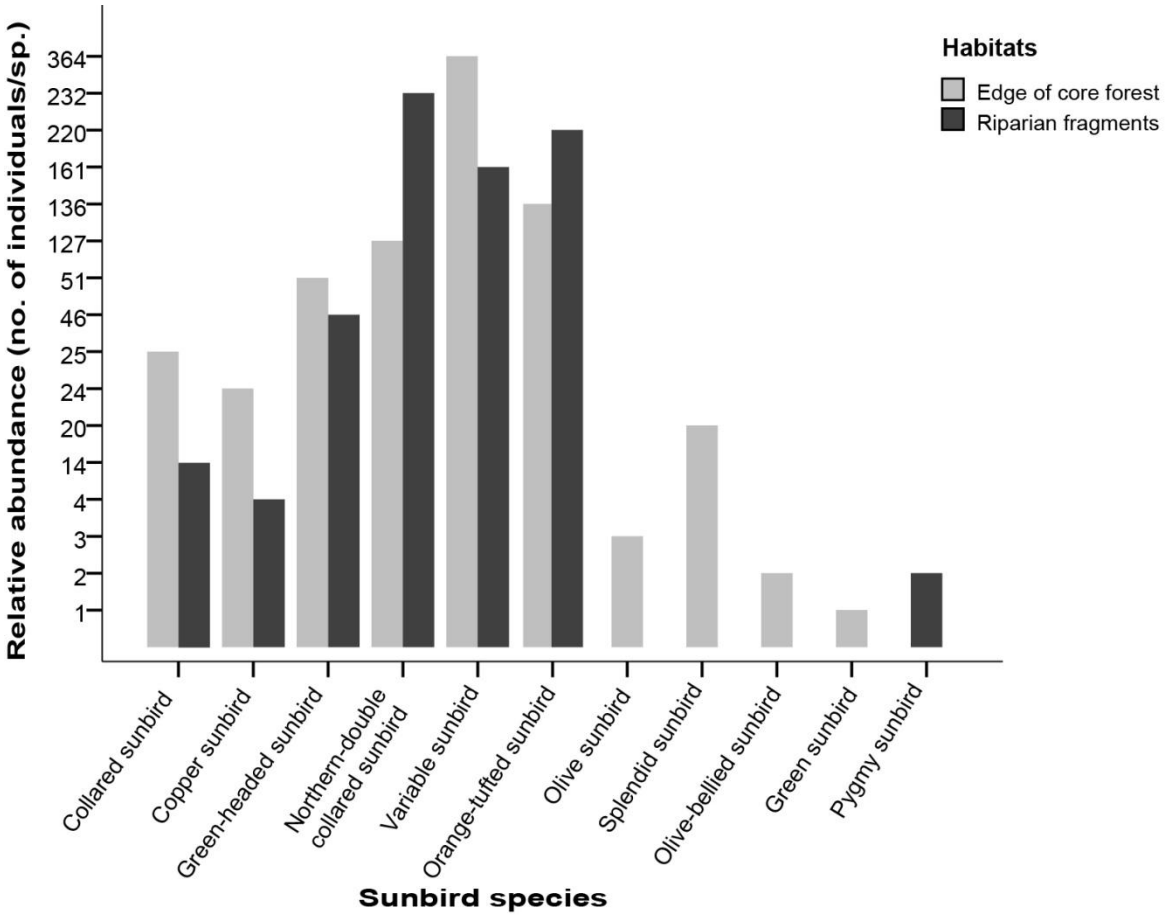



Figure 2.4: Sunbird species distribution/abundance at Ngel Nyaki Forest Reserve. Bars represent relative abundance (i.e number of individuals of each sunbird species.

Table 2.2: Relative abundance (Pi) of sunbird species at Ngel Nyaki Forest Reserve

| S/n | Species | No. of individuals (forest edge) | Relative abundance (Pi) | No. of individuals (fragments) | Relative abundance (Pi) |
|---|---|---|---|---|---|
| 1 | Northern-double collared sunbird | 127 | 0.168658699 | 232 | 0.34167894 |
| 2 | Variable sunbird | 364 | 0.483399734 | 161 | 0.237113402 |
| 3 | Orange-tufted sunbird | 136 | 0.18061089 | 220 | 0.324005891 |
| 4 | Green-headed sunbird | 51 | 0.067729084 | 46 | 0.067746686 |
| 5 | Copper sunbird | 24 | 0.03187251 | 4 | 0.005891016 |
| 6 | Collared sunbird | 25 | 0.033200531 | 14 | 0.020618557 |
| 7 | Pygmy sunbird | 0 | 0 | 2 | 0.002945508 |
| 8 | Olive-bellied sunbird | 2 | 0.002656042 | 0 | 0 |
| 9 | Olive sunbird | 3 | 0.003984064 | 0 | 0 |
| 10 | Cameroon sunbird | 0 | 0 | 0 | 0 |
| 11 | Western-violet backed sunbird | 0 | 0 | 0 | 0 |
| 12 | Splendid sunbird | 20 | 0.026560425 | 0 | 0 |
| 13 | Green sunbird | 1 | 0.001328021 | 0 | 0 |
| | **Total** | **753** | | **679** | |

### 2.7.2: Sunbird species diversity at Ngel Nyaki forest reserve

Based on all assessments (line transect, mist net capture, and flower visitation), I found 11 species occurring with varying degrees of abundance. Eight of these 11 species were recorded during periodic line transect surveys (Table 2.2). Three species (olive-bellied sunbird *Cinnyris chloropygius*, olive sunbird *Cyanomitra olivaceus* and green sunbird *Anthreptes rectirostris*) were captured during mist-netting and pollen load assessment.

However, the Cameroon sunbird *Cyanomitra oritis*, and western violet-backed sunbird *Anthreptes longuemarei*, were never encountered in the study sites during any of the experimental assessments, yet based on regional distribution and local checklist these species occur at Ngel Nyaki (Borrow & Demey, 2001; Tony Disley unpublished checklist). In terms of generic differentiation, our results show that of the eight occurring genera in Nigeria, five genera occur at Ngel Nyaki forest. *Cinnyris*, the most common genus in the forest reserve had six out of the 11 known species in this genus that occur in Nigeria. While *Cyanomitra* the

second most abundant genus in the reserve, was represented by three out of four species that occur in Nigeria (Appendix 2.2).

**a)** Northern double collared sunbird (adult male)

**b)** Olive sunbird (adult)

**c)** Orange tufted sunbird (adult male)

**d)** Green headed sunbird (adult male)

**e)** Variable sunbird (male)

**f)** Olive-bellied sunbird (adult female)

**g)** Green sunbird

**h)** Splendid sunbird

**(Figure 2.5 a-h): Sunbird species diversity. (photo credit: Charles Nsor)**

## 2.8: Discussion

### 2.8.1: Sunbird species diversity

In this survey, we recorded 11 of the 27 species of sunbirds known to occur in Nigeria. Ngel Nyaki forest therefore, accounts for about 40.7 % of the total species of sunbirds in Nigeria and about 33.3 % in the West African sub-region (Borrow & Demey, 2001; Mann & Cheke, 2010).

**Ecological implication**

Empirical evidence suggests that the stability of communities over time increases with diversity (Cottingham et al., 2001; Tilman, 1996; Tilman, 1999; Valone & Hoffman, 2003). This implies that knowledge of species diversity of a given locality or ecological community can inform on the functional dynamics and stability of that particular community. Ecological processes such as pollination will benefit largely from the high diversity of sunbirds recorded in this forest, since sunbirds contribute greatly to the reproduction of most flowering plant species (Geerts & Pauw, 2009; Janeček et al., 2011; Janecek et al., 2007; Janeček et al., 2012; Weston et al., 2012). From my results, I contend that in terms of sunbird diversity, the bird-tree community structure in this forest is bound to be temporally stable, as our results indicate a relatively high level of diversity of sunbird species compared to other studies across similar landscapes (Abalaka & Manu, 2007; Janeček et al., 2012; Imong, 2007; Manu et al., 2010). To the best of my knowledge, this is the highest record of sunbird species diversity relative to forest area surveyed in Nigeria.

### 2.8.2: Endemism

The occurrence of the northern-double collared sunbird *Cinnyris reichenowi* and the orange-tufted sunbird *Cinnyris bouvieri* at Ngel Nyaki forest and probably other adjoining forests within their range on the Mambilla Plateau makes these forests the only other landscape in Nigeria besides Obudu plateau home to these species (Borrow & Demey 2001; Manu et al., 2010). This finding further strengthens and supports the view of a high degree of endemism and diversity of birds in most forest within this eco-region (Elgood et al., 1994; Ezealor, 2001; Manu et al., 2010; Stattersfield et al.,1998). Ngel Nyaki forest therefore, could serve as an ecological refuge for many other bird species and a crucial habitat for the survival of sunbird species, especially those that are endemic or range restricted, should the need arise for their protection and conservation.

### 2.8.3: Rarity

Although some sunbird species such as the northern-double collared sunbird, the orange-tufted sunbird, and variable sunbird, recorded in this assessment fall among the most common bird species encountered daily at Ngel Nyaki (personal observation), other species such as the splendid sunbird *Cinnyris coccinigaster*, collared sunbird *Hedydipna collaris*, olive sunbird and olive-bellied sunbird were rarely encountered. However species such as the Cameroon sunbird and western violet- backed sunbird were never seen regardless of the fact that recent and past literatures suggest they are present in this forest. (Borrow & Demey, 2001). The absence of these species in our records suggests that they are probably highly seasonal, very elusive or rare in this forest. Not finding these species at Ngel Nyaki could also be because they have shifted range or decreased in population such that they have become very difficult to observe. This finding reflects the views of Hughes et al. (1997), that rate of loss of populations is far higher than rates of loss of species. While these species may be depleted completely for all we know, we might miss the opportunity of reversing possible

decline and subsequent local extinction of these species unless a detailed population level assessment is carried out to determine their population and detect any threats they might be facing at Ngel Nyaki Forest.

These findings could serve as a warning sign for possible threats to Cameroon sunbird globally considering the similarities between Ngel Nyaki and most of the Cameroon highlands where Cameroon sunbird is a common endemic. We could run the risk of moving from a declining population to global extinction if urgent monitoring actions are not taken in the near future.

One remarkable finding from this survey was the record of the green sunbird (fig. 2.5 g), a species that was previously unknown at Ngel Nyaki and the entire Mambila plateau region (Borrow & Demey, 2001). Although apparently rare at Ngel Nyaki based on my survey, the sighting of this species further confirms our view that avian diversity at Ngel Nyaki forest has been under-explored.

### 2.8.4: Abundance and habitat preference

Sunbird species varied in their spatial distribution and relative abundance. Variable sunbird *Cinnyris venustus* was the most abundant species throughout the period of investigation (2012 to 2014) (Figure 2.4); while northern-double collared sunbird and orange-tufted sunbird were the second and third most abundant species respectively (Figure 2.4).

More species were found in the core forest (ten species) than the fragment (seven species) (Table 2). This perceived display of habitat preference suggest that six species of the eleven recorded in this study have perhaps adapted to both fragmented and continuous habitats (forest core). These species: northern double collared sunbird, orange tufted sunbird, variable sunbird, copper sunbird, collared sunbird and the green headed sunbird were also the group

with three of the most abundant species in the forest. While my results suggest that the afore-mentioned species are habitat generalists, it is less clear whether the other five species, pygmy sunbird, green sunbird, olive sunbird, olive bellied sunbird and the splendid sunbird are habitat specialists. It is difficult to say at this stage; more periodic sampling across all seasons, over a couple of years would be required to confirm the distribution status of these species. At this stage of my investigation, I can only conclude that species that were only found in the core forest such as green sunbird, olive sunbird and olive-bellied sunbird were certainly rare at Ngel Nyaki forest, although this does not preclude their sensitivity to fragmented habitats. But, some studies (e.g. Burgess et al., 2005, Kelly et al., 2000), reported a higher visitation rate by some bird species at the edges of fragmented landscape, while (Stouffer & Bierreggaard, 1995), showed that understory hummingbirds persist in a matrix of fragments, secondary growth and large forest patches for several years. These studies (Burgess et al., 2005; Kelly et al., 2000; Stouffer & Bierreggaard, 1995), therefore suggest that some bird species are less sensitive to fragmentation. Burgess et al. (2005) listed eight studies where positive effects of fragmentation (i.e. increased visitation rates and fruit-set) have been recorded. However, my result is consistent with past studies that have attributed loss of species diversity to the negative effects of fragmentation (Manu et al., 2007, Norris et al., 2010; Dami et al., 2014; Debinski & Holt, 2000; Hagen et al., 2012; Mayfield et al., 2010; Pineda & Halffter, 2004; Wilcox & Murphy, 1985).

Species evenness (i.e. numerical equality of species in a given community) was low (Table 2.2), implying that some sunbird species were relatively more abundant in distribution. The difference in sunbird species abundance is reflected in the wide margin of difference between effective number of species and species richness (section 2.7.1.), in both habitat types. From the network perspective, the relative abundances of sunbird species gives an idea of the

number of possible sunbird-tree interactions that could potentially occur at Ngel Nyaki forest (Vazquez & Aizen, 2003). This assumption is based on the view that the number of interactions per species is strongly correlated with a species' relative abundance (Vazquez et al., 2005). In addition, we can also predict the nature of inter and intra-specific interactions between sunbird species and tree species, especially in relation to resource utilisation (e.g. floral resources).

While sunbird species differed in their distribution and abundance numerically (Table 2.2); overall species distribution followed a generalised pattern at least for the three most abundant species (Variable sunbird, northern-double collared sunbird, and orange-tufted sunbird) (Table 2.2 and appendix 2.7).

From my results (Figure 2.4 and table 2.2), it does appear that sunbird species showed a preference in their distribution across the two habitat types. For instance, variable sunbird, despite being the most abundant species in the reserve, was not dominant in both habitats. It was however, the most sighted and abundant species along the edge of the core forest throughout the entire period of the assessment. Northern double-collared sunbird, the second most common species overall at Ngel Nyaki forest was the most abundant in the riparian fragment (Figure 2.4). Interestingly, variable sunbird and northern double-collared sunbird were the third most common bird species in fragment and edge of core forest respectively. However, orange-tufted sunbird was the second most abundant species in the riparian fragments and edge of core forest. This implies that orange-tufted sunbird was more abundant than northern double-collared sunbird in the edge of core forest and variable sunbird in the fragment (Figure 2.4 and table 2.2).

While the above pattern of distribution of the three most abundant species could be driven by several factors such as availability of food, suitable breeding and roosting sites, we found

strong evidence for a combination of these factors in the distribution of variable sunbird in the reserve during the period of the assessment.

Each year one or more nest and even nestlings in 2014 of variable sunbird were discovered at the grassland habitats near the forest edge during transect observations (Appendix 2.4 and 2.5). These birds built their nests about two feet above the ground on grass stems and spent a great deal of time hawking for insects to feed their young, hence their relative abundance during this period (January-February) and within this part of the forest. I also noticed that during this time *Anthonotha. noldeae*, one of the most common tree species in the edge of the core forest was in full bloom. This tree species is one of the most sunbird visited tree species in the reserve (Nsor & Chapman, 2013) and attracts all kinds of insects as well as birds. The timing and synchronisation of variable sunbird breeding with the flowering season of *A. noldeae* could be an indication of the ecological significance of this tree species in the reproductive well being of variable sunbird at Ngel Nyaki. In addition variable sunbird nest were found along the edges of the core forest a few metres away from *A. noldeae* in all locations where they were sighted. Interestingly, *A. noldeae* is almost completely absent in the riparian fragments apart from two or three trees; this is probably the reason why we could not find a single nest in the fragment.

However, we lack empirical data to support any strong claim of habitat preference for this species and the rest of the sunbird species especially those that were restricted to just one of the habitats. It is most likely that the pattern of distribution of sunbird species at Ngel Nyaki forest is only a response to spatio-temporal variation in abundance of resources and fitness requirements and not preference for a specific habitat. This line of thought (especially fitness requirements), is supported by the seasonal abundance and almost ubiquitous presence of variable sunbird as highlighted above. The high demand for energy to support the nestlings

probably drives this species to look for insects to supplement the high-protein requirements of the nestlings. This additional dietary requirement is probably the reason for their relatively high abundance in the forest edge as they had to hunt for insects almost all day long. Similar findings have been made by past studies (Burgess et al., 2005), where higher visitation rates and fruit set were recorded more in edges of fragmented forest than in the core forest (Burgess et al., 2005).

Species such as green sunbird, splendid sunbird, olive bellied sunbird, and olive sunbirds were only recorded in the core forest. Although the scope of this assessment did not include testing habitat variables responsible for distribution and preferences by sunbird species, the results suggest that habitat structure (patch size) and composition, particularly resource availability could be a proximate factor driving the spatial distribution of sunbird species at Ngel Nyaki forest (Dami et al., 2014; Wilcove et al., 1986).

### 2.8.5: Range shifts and new records of bird species

The results of this study suggest that this forest has more potential for bird conservation than is presently known. Although acknowledge by BirdLife International as an IBA and EBA (Important Bird Area and Endemic Bird Area) respectively (Stattersfields et al., 1998), my findings indicate that there is a lot more in this forest than present records suggest. For instance, during mist-netting, six species that were previously excluded from this geographical region (see Borrow & Demey, 2001), were captured or seen during field observations (Appendix 2.2). However, the shift or extension in range of this species seems quite negligible (personal discussions with Demey), and may not require correcting the existing distribution maps, as this species were previously sighted only a few kilometres outside the Mambilla plateau region and were thus not included as occurring in this forest and the Mambilla plateau (see Borrow & Demey, 2001). However, this non significant extension

in range could imply that anthropogenic pressures from other places where these birds occur could be mediating the migration of these species. The most remarkable shift in range was the presence of Bamenda apalis *Apalis bamendae*, (Nsor et al., 2014) a species formerly considered as being endemic to the Bamenda highlands and Adamawa Plateau of North-West Cameroon (Borrow & Demey, 2001). These findings suggest that Ngel Nyaki forest may be home to many other species probably of global concern.

### 2.8.6: Conclusion and recommendations

Although slight differences were found in species diversity and richness between the two habitats, more work (sampling of rare species) needs to be done to determine whether this differences are driven by habitat effects. My results provide the background and framework for the development of the sunbird-tree pollination network which in terms of trophic differentiation (sunbird and tree species), already provides a preview of the structural composition of one group (sunbird species). The generalised pattern of distribution of species, low species evenness and relatively high species diversity derived from the results of this assessment suggest that sunbird-tree interactions would not be limited by spatial distribution at least for most species that are habitat generalist. Ngel Nyaki forest is indeed rich in sunbird diversity, probably the richest in the entire Mambilla plateau.

### Recommendations

The sighting and discovery of species previously unknown to this forest and region, calls for more intensive effort to optimise the full potential of this forest. In the light of this, I recommend a year-round comprehensive avian diversity/abundance study at Ngel Nyaki forest.

More effort should be geared towards prevention of indiscriminate bush-burning and encroachment into the core-forest by Fulani cattle-herders. The destructive activities of Fulani cattle herders threatens the reproductive wellbeing of ground/grass-nesters such as variable sunbird and a host of other bird species that make use of the grassland habitat at Ngel Nyaki forest.

# APPENDICES

Appendix 2.1: Generic distribution of sunbird species at Ngel Nyaki relative to Nigeria

| S/n | Genus | Species at Ngel Nyaki | Total no. of species in Nigeria |
|---|---|---|---|
| 1 | Cyanomitra | 3 | 4 |
| 2 | Anthreptes | 2 | 3 |
| 3 | Deleornis | 0 | 1 |
| 4 | Anthodiaeta | 1 | 1 |
| 5 | Anabathmis | 0 | 1 |
| 6 | Chalcomitra | 0 | 4 |
| 7 | Cinnyris | 6 | 11 |
| 8 | Hedydipna | 1 | 1 |

Appendix 2.2: List of new records for Ngel Nyaki forest reserve from mist netting survey.

| S/n | Species | Scientific Name | Remark |
|---|---|---|---|
| 1 | Green Sunbird | *Anthreptes rectirostris* | New in range |
| 2 | Bamenda Apalis | *Apalis bamendae* | First record in Nigeria |
| 3 | Brubru | *Nilaus afer* | New in range |
| 4 | White Bellied-Tit | *Parus albiventris* | New in range |
| 5 | Red bellied Paradise Flycatcher | *Terpsiphone batesi* | New in range |
| 6 | Black Bee-eater | *Merops gularis* | New in range |

Appendix 2.3: Status of Sunbird species in Nigeria relative to Ngel Nyaki. Of the 13 notable species at Ngel Nyaki, 11 were recorded in this study while two species (Cameroon sunbird and Western-violet backed sunbird) included below were absent throughout the study.

| S/N | SPECIES | SCIENTIFIC NAME | GENUS | PRESENCE @ NGEL NYAKI | LOCAL STATUS (Ngel Nyaki) | COUNTRY STATUS |
|---|---|---|---|---|---|---|
| 1 | Western Violet backed Sunbird | Anthreptes longuemarei | Anthreptes | Yes | Resident but not common | Common regionally |
| 2 | Brown Sunbird | Anthreptes gabonicus | Anthreptes | No | Not recorded | Very rare resident |
| 3 | Pygmy Sunbird | Anthodiaeta platura | Anthodiaeta | Yes | Breeding visitor | Seasonal migrant to common resident |
| 4 | Fraser's Sunbird | Deleornis fraseri | Deleornis | No | Not found | Common resident in Southern Nigeria |
| 5 | Olive Sunbird | Cyanomitra olivaceus | Cyanomitra | Yes | Resident but uncommon | Common resident |
| 6 | Collared Sunbird | Hedydipna collaris | Hedydipna | Yes | Resident but uncommon | Common Resident |
| 7 | Bates Sunbird | Cinnyris batesi | Cinnyris | No | Not recorded | Regionally common to uncommon |
| 8 | Little Green Sunbird | Anthreptes seimundi | Anthreptes | No | Not Recorded | Uncommon regional Resident |
| 9 | Buff-throated Sunbird | Chalcomitra adelberti | Chalcomitra | No | Not recorded | Uncommon regional resident |
| 10 | Reichenbach's Sunbird | Anabathmis reichenbachii | Anabathmis | No | Not Recorded | Rare resident |
| 11 | Green-headed Sunbird | Cyanomitra verticalis | Cyanomitra | Yes | Resident but uncommon | Common resident |
| 12 | Cameroon Sunbird | Cyanomitra oritis | Cyanomitra | Yes | Uncommon resdident | Range restricted |
| 13 | Blue-throated brown Sunbird | Cyanomitra cyanolaema | Cyanomitra | No | Not recorded | Uncommon resident |
| 14 | Camelite Sunbird | Chalcomitra fuliginosa | Chalcomitra | No | Not recorded | Very rare resident |
| 15 | Green throated Sunbird | Chalcomitra rubescens | Chalcomitra | No | Not recorded | Uncommon regional resident |
| 16 | Scarlet chested Sunbird | Chalcomitra senegalensis | Chalcomitra | No | Not recorded | Common resident |
| 17 | Variable Sunbird | Cinnyris venustrus | Cinnyris | Yes | Resident and partial migrant | Common resident, partially migratory |
| 18 | Tiny Sunbird | Cinnyris minullus | Cinnyris | No | Not recorded | Very Rare |
| 19 | Olive bellied Sunbird | Cinnyris chloropygius | Cinnyris | Yes | Partial migrant | Common resident, partially migratory |
| 20 | Northern Double Collared Sunbird | Cinnyris reichenowi | Cinnyris | Yes | Most common resident | Range-restricted |
| 21 | Orange tufted Sunbird | Cinnyris bouvieri | Cinnyris | Yes | Very common resident | Range restricted |
| 22 | Copper Sunbird | Cinnyris cupreus | Cinnyris | Yes | Uncommon resident | Common resident |
| 23 | Splendid Sunbird | Cinnyris coccinigastrus | Cinnyris | Yes | Uncommon resident | Common resident |
| 24 | Beautiful sunbird | Cinnyris pulchellus | Cinnyris | No | Not Recorded | Common regional resident |
| 25 | Superb Sunbird | Cinnyris superbus | Cinnyris | No | Not Recorded | Rare resident |
| 26 | Johanna's Sunbird | Cinnyris johannae | Cinnyris | No | Not Recorded | Very rare resident |
| 27 | Green Sunbird | Anthreptes rectirostris | Anthreptes | Yes | Very rare | New in range |

Appendix 2.4: Nest of variable sunbird *C. venustus* found near the field station in February, 2012.

Appendix 2.5: Nestlings of variable sunbird found in a grass field about 30 metres from the core forest, February, 2014.

Appendix 2.6: Calculation of Effective number of species.

$$\exp\ (\mathrm{H'})\ or \exp\ (-\sum_{i=1}^{s} p_i log_e p_i)$$

With

$$-\sum_{i=1}^{s} p_i log_e p_i$$

= 0.65, 0.60, and 0.65. I calculated the effective number by obtaining the exponential values of each Shannon Wiener Index thus; exp (0.65) = 1.92, exp (0.60) = 1.82 and exp (0.65) = 1.92; for core, fragment and overall (Ngel Nyaki Forest Reserve) diversity respectively.

Appendix 2.7: Species richness and true diversity of the core forest edge and fragments. Note: 1 indicates presence of a species, while 0 indicates absence.

| Species | Core forest edge | Fragments |
|---|---|---|
| Northern-double collared sunbird | 1 | 1 |
| Variable sunbird | 1 | 1 |
| Orange-tufted sunbird | 1 | 1 |
| Green-headed sunbird | 1 | 1 |
| Copper sunbird | 1 | 1 |
| Collared sunbird | 1 | 1 |
| Pygmy sunbird | 0 | 1 |
| Olive-bellied sunbird | 1 | 0 |
| Olive sunbird | 1 | 0 |
| Cameroon sunbird | 0 | 0 |
| Western-violet backed sunbird | 0 | 0 |
| Splendid sunbird | 1 | 0 |
| Green sunbird | 1 | 0 |
| **Total number of species (species richness)** | **10** | **7** |
| **Effective number of species (true diversity)** | **1.92** | **1.82** |

From the table above, four species are unique to the core forest while one species is unique to the fragment. Based on the above, Jaccard similarity index is calculated using the formula below:

$$C_j = \frac{a}{(a+b+c)}$$

$C_J$ = Jaccard similarity index, a = total number of species in both habitats, b = species unique to core habitat, c = species unique to the fragments.

$$C_j = \frac{a}{(a+b+c)} = \frac{11}{(11+4+1)} = \frac{11}{16} = 0.68$$

$C_J$ = 0.68 (i.e. 68 % similarity in species diversity between the core and fragmented habitats).

## REFERENCES


Abalaka, J. I., & Manu, S. A. (2007). Factors affecting forest bird diversity and recent avifaunal changes in the degrading Kagoro-Nindam forest reserves, Kaduna, Nigeria. *Ostrich*, 78(2), 233-238.

Ash, J., Dowsett, R., & Dowsett-Lemaire, F. (1989). New ornithological distribution records from eastern Nigeria. *Tauraco Research Report*, 1, 13-27.

Atauri, J. A., & de Lucio, J. V. (2001). The role of landscape structure in species richness distribution of birds, amphibians, reptiles and lepidopterans in Mediterranean landscapes. *Landscape ecology*, 16(2), 147-159.

Bibby, C. J., Burgess, N. D., Hill, D. A., & Mustoe, S. H. (2001). Bird Census Techniques. Academic Press, London. 302 pp

BirdLife International. (2013). *State of the World's Birds*: Indicators for our changing world. Cambridge, UK, BirdLife International, Pg 9.

Borrow, N., & Demey, R. (2001). *A Guide to the Birds of Western Africa*. Princeton University Press.

Burgess, V. J., Kelly, D., Robertson, A. W., & Ladley, J. J. (2006). Positive effects of forest edges on plant reproduction: literature review and a case study of bee visitation to flowers of *Peraxilla tetrapetala* (Loranthaceae). *New Zealand Journal of Ecology*, 30 (2), 179-190.

Chapman, J. D., & Chapman, H. M. (2001) *The Forests of Taraba and Adamawa States, Nigeria. An Ecological Account and Plant Species Checklist*. University of Canterbury, Christchurch, New Zealand.

Cottingham, K., Brown, B., & Lennon, J. (2001). Biodiversity may regulate the temporal variability of ecological systems. *Ecology Letters*, 4(1), 72-85.

Dami, F. D., Mwansat, G. S., & Shiiwua, A. M. (2014). The Effect of Fragmentation and Land Use Types on Bannerman's Weaver Ploceus bannermani (A Globally-Threatened Bird Species) on the Obudu Plateau, Southeast Nigeria. *Journal of Natural Sciences Research*, 4(19), 91-97.

Debinski, D. M., & Holt, R. D. (2000). A survey and overview of habitat fragmentation experiments. *Conservation Biology*, 14(2), 342-355.

Diamond, J. M., & Case, T. J. (1986). *Community Ecology*. Harper & Row New York.

Dowsett-Lemaire, F. (1989). The flora and phytogeography of the evergreen forests of Malawi I: Afromontane and mid-altitude forests. *Bulletin du Jardin botanique national de Belgique/Bulletin van de Nationale Plantentuin van Belgie*, 3-131.

Durant, J. M., Hjermann, D. O., Ottersen, G., & Stenseth, N. C. (2007). Climate and the match or mismatch between predator requirements and resource availability. *Climate Research*, 33, 271-283

Elgood, J. H., Heigham, J. B.,Moore, A. M., Nason, A. M., Sharland, R. E., & Skinner, N. J. (eds). (1994). *The Birds of Nigeria*, (2nd edition). BOU Checklist No. 4. Tring: British Ornithologists' Union.

Ezealor, A. (2001). Nigeria: Important Bird Areas in Africa and associated islands: priority sites for Conservation. *BirdLife Conservation series* (11), 673-682.

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., . . . Gibbs, G. C. (2005). Global consequences of land use. *Science*, 309(5734), 570-574.

Furness, R. W., & Greenwood, J. J. (1993). *Birds as Monitors of Environmental Change*. Chapman & Hall London.

Geerts, S., & Pauw, A. (2009). Hyper-specialization for long-billed bird pollination in a guild of South African plants: the Malachite Sunbird pollination syndrome. *South African Journal of Botany*, 75(4), 699-706.

Gregory, R. , Noble, D., Field, R., Marchant, J., Raven, M., & Gibbons, D. W. ( 2003). Using birds as indicators of biodiversity. *Ornis Hungarica*, 12(13), 11-24.

Gregory, R. D., Willis, S. G., Jiguet, F., Vorisek, P., KLvanova, A., van Streien, A., . . . Green, R. E. (2009). An indicator of the impact of climatic change on European bird populations. *PloS one*, 4(3), e4678.

Hagen, M., Kissling, W. D., Rasmussen, C., Cartensen, D. W., Dupont, Y. L., Kaiser-Bunbury, C. N., . . . Olesen, J. M. (2012). Biodiversity, species interactions and ecological networks in a fragmented world. *Advances in Ecological Research*, 46, 89-120.

Hall, P. (1976). The birds of Mambilla Plateau. *Bulletin of the Nigerian Ornithological Society*, **12**, 67-72.

Hinsley, S., & Bellamy, P. (2000). The influence of hedge structure, management and landscape context on the value of hedgerows to birds: a review. *Journal of environmental management*, 60(1), 33-49.

Hughes, J. B., Daily, G. C., & Ehrlich, P. R. (1997). Population diversity: its extent and extinction. *Science*, 278(5338), 689-692.

Imong, I. S. (2007). *Effects of Habitat Type and Anthropogenic Disturbance on the Density and Distribution of Birds in the Sankwala Mountains, Nigeria*, University of Jos. Masters Thesis.

IUCN. (2012). *IUCN Red List of Threatened Species*. Version 2012.2. International Union for the Conservation of Nature Gland, Switzerland.

Janeček, Š., Patacova, E., Bartos, M., Padysakova, E., Spitzer, L., & Tropek, R. (2011). Hovering sunbirds in the Old World: occasional behaviour or evolutionary trend? *Oikos*, 120(2), 178-183.

Janecek, S., Pesata, M., Hrazsky, Z., Bartos, M., Brom, J., Reif, J., . . . Bystricka, D. (2007). Importance of big pollinators for the reproduction of two Hypericum species in Cameroon, West Africa. *African Journal of Ecology*, 45(4), 607-607.

Janeček, Š., Pesata, M., Mikes, V., Patacova, E., Altman, J., Kantorova, J., . . . Brom, J. (2012). Food selection by avian floral visitors: an important aspect of plant–flower visitor interactions in West Africa. *Biological Journal of the Linnean Society*, 107(2), 355-367.

Jost, L. (2006). Entropy and Diversity. *Oikos*, 113(2), 363-375.

Kelly, D., J. J., Ladley, A. W., Robertson, & Norton, D. A. (2000). Limited forest fragmentation improves reproduction in the declining New Zealand mistletoe *Peraxilla tetrapetala* (Loranthaceae). 241-251 in A. G. Young and G. M. Clarke, editors. Genetics, demography and viability of fragmented populations. Cambridge University Press, Cambridge.

Kikvidze, Z., Pugnaire, F. I., Brooker, R. W., Choler, P., Lortie, C. J., & Michalet, R., Callaway, R. M. (2005). Linking patterns and processes in alpine plant communities: a global study. *Ecology*, 86(6), 1395-1400.

Klein, A. M., Vaissiere, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tschantke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, 274(1608), 303-313.

Maestre, F. T., Valladares, F., & Reynolds, J. F. (2005). Is the change of plant–plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. *Journal of Ecology*, 93(4), 748-757.

Maestre, F. T., Castillo-Monroy, A. P., Bowker, M. A., & Ochoa-Hueso, R. (2012). Plant species richness and ecosystem multifunctionality in global drylands. *Science*, 335(6065), 214-218.

Mann, C. F., & Cheke, R. A. (2010). *Sunbirds*: A guide to the sunbirds, flowerpeckers, spiderhunters and sugarbirds of the world. A&C Black.

Manu, S., Peach, W., & Cresswell, W. (2007). The effects of edge, fragment size and degree of isolation on avian species richness in highly fragmented forest in West Africa. *Ibis*, 149(2), 287-297.

Manu, S., Imong, I. S., & Cresswell, W. (2010). Bird species richness and diversity at montane Important Bird Area (IBA) sites in south-eastern Nigeria. *Bird Conservation International*, 20(3), 231-239.

Mayfield, M., Bonser, S. P., Morgan, J. W., Aubin, I., McNamara, S., & Vesk, R. A. (2010). What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. *Global Ecology and Biogeography*, 19(4), 423-431.

McKay, C., & Coulthard, N. (2000). The Kilum-Ijim Forests IBA in Cameroon: monitoring biodiversity using birds as indicators. *Ostrich*, 71(1-2), 177-180.

Memmott, J., Waser, N. M., & Price, M. V. (2004). Tolerance of Pollination Networks to Species Extinctions. *Proceedings: Biological Sciences*, 271(1557), 2605-2611.

Mulder, C., Bazeley-White, E., Dimitrakopolos, P. G., Hector, A., Schere-Lorenzen, M., & Schmid, B. (2004). Species evenness and productivity in experimental plant communities. *Oikos*, 107(1), 50-63.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403(6772), 853-858.

Norris, K., & Pain, D. J. (2002). *Conserving Bird Biodiversity*: general principles and their application, 7. Cambridge University Press.

Norris, K., Asase, A., Collen, B., Goekowski, J., Mason, J., Phalan, B., & Wade, A. (2010). Biodiversity in a forest-agriculture mosaic–The changing face of West African rainforests. *Biological Conservation*, 143(10), 2341-2350.

Noss, R. F. (1991). Landscape connectivity: different functions at different scales. Landscape linkages and biodiversity. Island Press, Washington, DC, USA, 27-39.

Nsor, C. A., & Chapman, H. M. (2013). A preliminary investigation into the avian pollinators of three tree species in a Nigerian Montane Forest. *Malimbus*, 35, 37-49.

Nsor, C. A., Nicodemus, E., & Bashiru U. (2014). First record of Bamenda Apalis *Apalis bamendae* for Nigeria. *Bulletin of African Bird Club* (Vol 21), No 1.

Orme, C.D.L., Davies, R. G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V. A., . . . Ridgely, R. S. (2005). Global hotspots of species richness are not congruent with endemism or threat. *Nature*, 436(7053), 1016-1019.

Osinubi, S. T., Vugeh, Y., Briskie, J. V., Ottosson, U., Brown, J. A., & Chapman, H. M. (2014). Association with riparian fragments by Yellow-breasted Boubou atroflavus indicates need for wider-scale forest matrix conservation. *Malimbus* 36(1), 47-57.

Padoa-Schioppa, E., Baietto, M., Massa, R., & Bottoni, L. (2006). Bird communities as bioindicators: the focal species concept in agricultural landscapes. *Ecological Indicators*, 6(1), 83-93.

Pauw, A., & Louw, K. (2012). Urbanization Drives a Reduction in Functional Diversity in a Guild of Nectar-feeding Birds. *Ecology and Society*, 17(2), 1-27.

Pearce, J., & Ferrier, S. (2001). The practical value of modelling relative abundance of species for regional conservation planning: a case study. *Biological Conservation*, 98(1), 33-43.

Pineda, E., & Halffter, G. (2004). Species diversity and habitat fragmentation: frogs in a tropical montane landscape in Mexico. *Biological Conservation*, 117(5), 499-508.

Pringle, R. M., Doak, D. F., Brody, A. K., Jocqué, R., & Palmer, T. M. (2010). Spatial pattern enhances ecosystem functioning in an African savanna. *PLoS biology*, 8(5), e1000377.

Purvis, A., Gittleman, J. L., Cowlishaw, G., & Mace, G. M. (2000). Predicting extinction risk in declining species. *Proceedings. Biological sciences / The Royal Society*, 267(1456), 1947-1952.

Purvis, A., & Hector, A. (2000). Getting the measure of biodiversity. *Nature*, 405(6783), 212-219.

Rietkerk, M., Dekker, S. C., de Ruiter, P. C., & van de Koppel, J. (2004). Self-organised patchiness and catastrophic shifts in ecosystems. *Science*, 305(5692), 1926-1929.

Sechrest, W., Brooks, T. M., da Fonseca, G. A., Konstant, W. R., Mittermieir, R. A., Purvis, A., . . . Gittleman, J. L. (2002). Hotspots and the conservation of evolutionary history. *Proceedings of the National Academy of Sciences*, 99(4), 2067-2071.

Stattersfield, A., Crosby, M., Long, A., & Wege, D. (1998). *Endemic Bird Areas of the World*: priorities for biodiversity conservation, BirdLife International, Cambridge, UK.

Stouffer, P. C. & Bierregaard R. O. (1995). Effects of forest fragmentation on understory hummingbirds in Amazonian Brazil. *Conservation Biology* (9), 1085-1094.

Thomas, D. W., Blondel, J., Perret, P., Lambrechts, M. M., & Speakman, J. R. (2001). Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. *Science*, 291(5513), 2598-2600.

Tilman, D. (1996). Biodiversity: population versus ecosystem stability. *Ecology*, 77(2), 350-363.

Tilman, D. (1999). The ecological consequences of changes in biodiversity: a search for general principles 101. *Ecology*, 80(5), 1455-1474.

Usieta, H. O., Manu, S. A., & Ottosson, U. (2013). Farmland conservation in West Africa: how do hedgerow characteristics affect bird species richness? *Bird Study*, 60(1), 102-110.

Valone, T. J., & Hoffman, C. D. (2003). A mechanistic examination of diversity-stability relationships in annual plant communities. *Oikos*, 103(3), 519-527.

Vázquez, D. P., & Aizen, M. A. (2003). Null model analyses of specialisation in plant-pollinator interactions. *Ecology*, 84(9), 2493-2501.

Vázquez, D. P., Blüthgen, N., Cagnolo, L., & Chacoff, N. P. (2009). Uniting pattern and process in plant-animal mutualistic networks: a review. Oxford University Press, England, pp. 1445-1457.

Vázquez, D. P., Lomascolo, S. B., Maldonado, M. B., Chacoff, N. P., Dorado, J., Stevani, E. L., & Vitale, N. L. (2012). The strength of plant-pollinator interactions. *Ecology*, 93(4), 719-725.

Vazquez, D. P., Melian, C. J., Williams, N. M., Bluthgen, N., Krasnov, B. R., & Poulin, R. (2007). Species abundance and asymmetric interaction strength in ecological networks. *Oikos*, 116(7), 1120-1127.

Vázquez, D. P., Morris, W. F., & Jordano, P. (2005). Interaction frequency as a surrogate for the total effect of animal mutualists on plants. *Ecology Letters*, 8(10), 1088-1094.

Vázquez, D. P., Poulin, R., Krasnov, B. R., & Shenbrot, G. I. (2005). Species Abundance and the Distribution of Specialisation in Host-Parasite Interaction Networks. *Journal of Animal Ecology*, 74(5), 946-955.

Weston, K. A., Chapman, H. M., Kelly, D., & Moltchanova, E. V. (2012). Dependence on sunbird pollination for fruit set in three West African montane mistletoe species. *Journal of Tropical Ecology*, 28(2), 205-213.

Wilcove, D. S., McLellan, C. H., & Dobson, A. P. (1986). Habitat fragmentation in the temperate zone. *Conservation biology*, 6, 237-256.

Wilcox, B. A., & Murphy, D. D. (1985). Conservation strategy: the effects of fragmentation on extinction. *American naturalist*, 879-887.

## CHAPTER THREE

**How good a proxy is bird - flower visitation to bird pollination? Comparing a plant-sunbird visitation network with a plant-sunbird pollen transport network in Ngel Nyaki forest.**


## ABSTRACT

Understanding the functional properties of plant-animal pollination networks has historically focused on insects and used flower visitation rates to predict pollination effectiveness. This approach reflects the abundance of insect-flower pollinator data sets relative to other plant-animal interactions. Moreover it is notoriously difficult to measure pollination effectiveness so that most plant-pollinator networks are inaccurate and better reflect plant-animal visitation networks.

Here I used a null model approach to compare a sunbird-flower visitation network with sunbird- pollen transport network. I created the visitation network based on the visitation frequency of seven sunbird species to 14 tree species and the sunbird-pollen transport network by quantifying the number of pollen grains of each flower species carried on the bodies of each sunbird species. I hypothesised that tree species in the pollen transport network (PTN) will be a subset of those in the flower visitation network (FVN).

To compare the nestedness of the visitation and pollen transport networks, I compared the observed nestedness of each network with values from two null models each. I found more nestedness than we would expect by chance. The PTN had a higher nestedness than the FVN. Other network descriptors such as connectance and network level specialisation, revealed little variations between the two networks. There was a positive correlation between the FVN and PTN, despite 64% dissimilarity in species composition. This positive correlation suggests

that species that were unique to each network were less crucial with regards to pollination than the species common to both networks. However, some species that visited trees less frequently transported more pollen on average than most frequent flower visitors.

Our findings suggest that while visitation networks approximate pollination networks to a large extent, measuring pollination effectiveness will significantly alter nestedness and therefore conclusions drawn from such analyses.

## 3.0: Introduction

In this chapter, I investigate how good a proxy is a sunbird-tree *visitation* network to a sunbird-tree *pollen transport* network, by comparing the network structures (i.e. the pattern and arrangement of interacting species in a given interaction network). My approach was based on the supposition that if flower visitation does reflect pollen transport, then birds that visit particular tree species with a high frequency would transport the majority of their pollen. However not every contact between a bird and a flower represents a pollination event because birds also visit flowers as nectar thieves, florivores, and/or to prey upon other visitors such as insects (Popic et al., 2013). The inclusion of these interactions that may have variable effects on host fitness often results in networks that do not truly reflect pollination. In the light of this, it is necessary to determine the extent to which visitation networks reflect pollination networks.

### Network indices

Memmott (1999) constructed the first plant-pollinator network based on visitation frequencies to illustrate how existing methods of web construction and analysis can be applied to plant-pollinator systems. This approach to network theory (Memmott, 1999)

generated a surge of interest in mutualistic network properties leading to the development of metrics to describe network structure (Almeida-Neto et al., 2008; Atmar & Patterson, 1993; Brualdi & Sanderson, 1999; Dormann et al., 2009). Network structure refers to the pattern and arrangement of links (number of realised interactions) and nodes (species) in a given interaction. Analyses of network properties have lead to insights into when communities of mutualists can withstand perturbations and which properties might affect the probability of extinction for species (James et al., 2012; Saavedra et al., 2011), (see Chapter five).

While several different indices have been developed to describe network structure and from that, predict the ability of networks to withstand perturbations, two of them, 'connectance' (Jordano, 1987; Jordano et al., 2003), and 'nestedness' are particularly useful (Bascompte et al., 2003; Saavedra et al., 2011). Connectance describes the total number of links per network size. Nestedness is a property, or pattern associated with such networks such that specialist species (those with fewer interactions) are always associated with generalist ones (species with more interactions). If the network is highly nested then the specialist species interact with species that form well defined subsets of the species with which common/generalist species interact. Nestedness is an important and common feature of most interaction networks (Bascompte et al., 2003). This concept has been used to compare network structure across diverse ecological systems (Alarcón, 2010), in describing patterns of community organisation through interaction networks (Araujo et al., 2010), for assessing biodiversity (Fleishman et al., 2007), to illustrate community level response to anthropogenic threats (Fortuna & Bascompte, 2006; McQuiad & Britton, 2013) and for evaluating network persistence (i.e. the ability to withstand disturbance without collapse) and species survival (Saavedra et al., 2011; Vidal et al., 2014).

**Visitation frequency as a proxy for pollination effectiveness**

Explorations of the functional properties of plant-animal pollination networks have historically focused on insect – plant interactions and have used flower visitation rates as a proxy for pollination effectiveness (Forup et al., 2008; Memmott, 1999; Vázquez et al., 2012). This approach is understandable because it is extremely difficult to quantify pollination success following a flower visit by an insect (Ne'eman et al., 2010) and it is easier to assume that all insect flower visits affect pollination. However this is not necessarily the case; insects and animals also visit flowers as florivores, nectar thieves and/or to prey on other visitors (e.g. birds preying on insects), while sometimes inadvertently pollinating at the same time (Popic et al., 2013). Sunbirds for instance are consummate flower robbers because they are behaviourally flexible (intelligent) and have long, sharp bills ideal for piercing corollas. Thus one might expect that a flower visitation and a pollen transport network will differ for this group of pollinators. While a quantitative flower visitor network is useful to determine interaction frequency among species, it does not completely describe a pollination network, because a true pollination network should ideally include rates of pollen pickup and deposition at appropriate and compatible stigmas. Therefore the fact that most pollination networks are developed from flower visitation frequencies means that they are only approximations of pollination networks and it is difficult to judge to what extent they reflect real pollination networks.

In order to understand how well a flower visitation network reflects a pollination network, it is necessary to compare the two. However, given the constraints associated with generating qualitative data for testing the robustness of proxies (Popic et al., 2013), further approximations are required. It is assumed that these are closer to real pollination networks than mere visitation frequencies. For example the collection of pollen by each visitor can be

noted (Alarcón, 2010; Vázquez et al., 2005) and even the deposition of pollen onto stigmas (King et al., 2013; Pellmyr et al., 2002). The resultant network is called a pollen transport network. A combination of the pollen transport network and the visitation frequency network can conveniently be described as a "pollination network".

**Aim of study**

The aim of this study was to compare two networks, one based on visitation frequency alone and the other on pollination efficiency (pollen transport). In order to compare network structure in terms of patterns and arrangement of species I used the indices described above, 'nestedness' and 'connectance'. To compare functionality (i.e. species' visitation frequency and pollen load transport) between the different species of sunbirds in their pollination effectiveness, I determined to what extent flower visitation approximated flower pollination. Specifically the aim was to compare a sunbird-tree visitation network with a sunbird –tree pollination network. While not perfect, I decided to use pollen pickup as a proxy for pollination (Alarcon, 2010; Vazquez et al., 2005).

**The specific objectives were**:

1. To use flower visitation data and pollen load data to infer the structure of sunbird-tree visitation and pollen transport network in a Nigerian Montane forest system.

2. To use network properties such as nestedness and connectance to compare the structural differences between the flower visitation and the pollen transport networks.

I tested the following hypothesis:

i) Flower visitation networks are a good reflection of pollen transport networks so that birds that visit flowers the most will also transport the most pollen.

ii) The tree species composition in the pollen transport network (PTN) will be a subset or similar in species composition to those of tree species in the flower visitation network (FVN).

iii) There is no difference in flower visitation frequency and quantity of pollen transported among species, and therefore the visitation and pollination networks will be symmetrical.

iv) Observed NODF (Nestedness based on overlap and decreasing fill) values for FVN and PTN would be similar with those obtained from 1000 randomised matrices of each of the observed networks.

## 3.1: Materials and Methods

### 3.1.1: Study Site (refer to the relevant sections in chapter 1)

**Ngel Nyaki Forest Reserve**

The study was conducted at Ngel Nyaki Forest Reserve (07$^{o}$ 05'N 11$^{o}$ 04'E) located towards the eastern edge of the Mambilla Plateau in Taraba state Nigeria (Figure 1.3, chapter 1) at an elevation of approximately 1550 m a.s.l (Chapman & Chapman, 2001). Ngel Nyaki Forest Reserve is 45 km$^2$ in extent, of which *c.*7.5 km$^2$ comprises montane/submontane forest (Chapman & Chapman 2001). The forest is surrounded by overgrazed grassland and savannah as well as associated riparian forests (Dowsett-Lemaire, 1989).

The fauna of Ngel Nyaki is part of the globally important Cameroon mountain range, as can be seen in the avifaunal composition, e.g. Cameroon sunbird *Cyanomitra oritis*, Bamenda apalis *Apalis bamendae*, Cameroon olive pigeon *Columba sjostedti*, Bannerman's weaver *Ploceus bannermani* etc. Some of these species like *Ploceus bannermani* are threatened with extinction (Birdlife International, 2013) while others are range-restricted and endemic species of high elevation forests, unique to the Ngel Nyaki/Cameroon montane eco-region (Fishpool & Evans, 2001; Manu et al., 2010). In addition to its status as an EBA (Endemic Bird Area) Ngel Nyaki forest is also one of the most species rich of the 27 IBAs (Important Bird Areas) in Nigeria (Fishpool & Evans, 2001; Manu et al., 2010).

### 3.1.2: Focal Observation

In order to develop a sunbird/tree flower visitation network I observed a total of five individual trees for each of 16 tree species during portions of the day when sunbirds are particularly active (6:30 am -12:30 pm, and 3:30 -5:30 pm). These observations were restricted to periods of peak flowering between 2011 and 2014 (Nigerian Montane Forest Project phenology data). Tree species were chosen based on availability of flowers and abundance of individual trees. However, effort was made to vary observation periods to address the disparity in flowering phenology (i.e. irregular flowering cycles of individuals of a given species) and season. The aim was to generate data that would be representative of all flowering trees in the forest. Each individual tree was monitored for a period of 20 minutes during each observation session (i.e. morning or evening), amounting to 40 observation minutes per day.

We positioned ourselves approximately 25 metres away from a focal tree to avoid possible distraction of the foraging activities of sunbird species. Each time birds were seen settling on the tree, we recorded their identity, time of detection or arrival, number of individuals, nature of interaction (antagonistic or mutualistic), number of flowers contacted and the time of departure.

To account for variation in spatial abundance and distribution of sunbird species, we selected focal trees from different parts of the forest. Trees were at least 100 metres away from each other. Individuals of each tree species were monitored for a total of 120 minutes (that is, three days of 40 minutes sessions per day). We alternated the order of observation across trees to account for any possible biases that may arise from time of day.

### 3.1.3: Mist-netting

In order to capture sunbird species for pollen load estimation, we used mist nets with mesh size 1.5, (ca 2 x 9 m, three and four-shelf) from Avinet Inc. Nets were set up along established flight paths of sunbirds within the vicinity of flowering tree species. We set up nets with minimal clearing of vegetation to reduce alteration of habitats. Trapping was conducted twice each day in the morning (6:30 am -12:30 pm) and evening (3:30 -5:30 pm). During each trapping session, which lasted for about four to six hours per session (morning or evening), nets were periodically checked at an interval of 20 minutes. A total of 209 hours, four minutes was spent during 38 days of trapping. Trapping was done for nine consecutive days in November, 2012, eighteen consecutive days between January and February, 2013, and 11 consecutive days in February, 2014. These periods coincided with peak periods of flower abundance to ensure availability of pollen. Approximately six hours was spent trapping each day depending on weather (High wind velocity was a limiting factor).

Pollen grains were compared with voucher specimens obtained from tree species within the vicinity of the mist nets for identification of the source. Pollen samples that were difficult to identify in the field were labelled and identified in the laboratory (Kearns & Inouye, 1993). We dabbed and rubbed the body of the sunbird (fore-head, bill, chin, belly and tail) with a 2 mm cube of fuchsin gel to remove as much pollen as possible for identification of the pollen to plant species. Each dabbed gel cube was then placed on a glass slide, melted and covered with a cover slip to produce a single layer of stained pollen grains. Slides were analysed at 40-100 x magnification and compared to reference samples taken from flowers within the study site where birds were captured. After identification, counted pollen was scored against the individual sunbird species it was obtained from. Some slides contained pollen from

different sources (heterospecific), while most slides contained pollen from a single plant. However, about 10% of pollen could not be identified to the level of species and were regarded as unknown.

Captured sunbirds were identified to species using field guides to birds of Western Africa (Borrow & Demey, 2001) and sexed (if mature).

Unique plastic colour bands (from Avinet Inc.) were placed on the bird's tarsi so as to track the pattern of movement of sunbird species and possibly determine how far they move pollen, in the event of recapture or sighting during focal observation at a separate time. We banded each bird after obtaining biometrics such as weight and bill length. We ensured that rings were placed in a manner that did not pose any risk of entrapment or hindrance to the bird's daily activity such as movement, growth and tissue enlargement.

### 3.2: Data Analysis

#### Network structure

First, I pooled the observed flower visits (cumulative visit by individuals of each species) to create a single pollinator by plant matrix for both visitation and pollen transport networks. For the FVN, the cell values represents the number of occasions individual sunbird visitors from species *S* were observed feeding on flowers of tree species *T* (Alarcon et al. 2008). Where *S* and *T* represents sunbird and tree species respectively (See Figure 3.1 below). This approach was repeated for the pollen load estimation network. Here cell values were represented by the number of conspecific pollen grains of tree species *T* carried by individuals of sunbird species *S.*

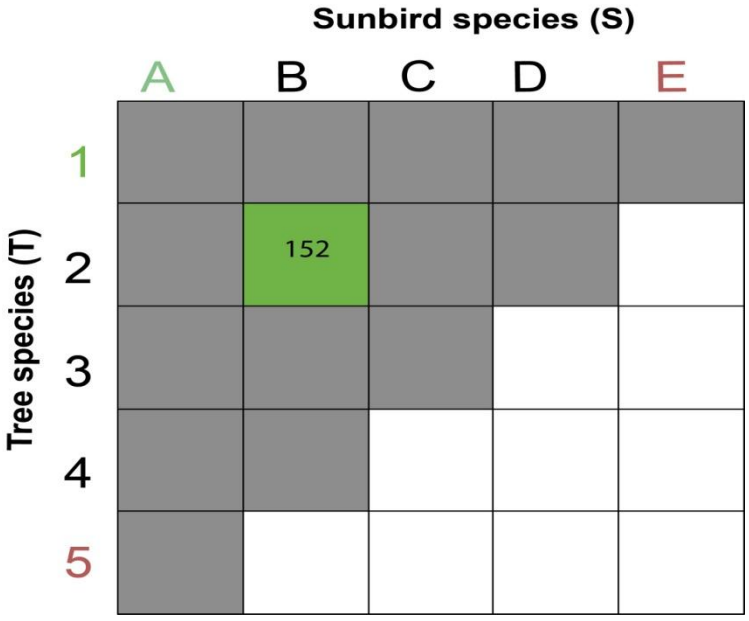



Figure 3.1: Hypothetical matrix showing matrix cell occupancy derived from interaction frequency between sunbird species B and tree species 2. Number of hypothetical interactions is highlighted in green (152 hypothetical interactions); Grey boxes represents interactions while white boxes indicates no interactions.

In order to construct the visitation and pollination networks and then compare the structural differences between them, I used the bipartite package in R (R statistical software, version 2.15.3, R development core team, 2013). I generated the web structures using the "plotweb" function (Figure 3.3 and 3.4) and calculated the network property nestedness for each network using the function "nestednodf", based on NODF metric (i.e. nestedness based on overlap and decreasing fill) (Almeida-Neto et al., 2008). Other structural and functional descriptors of networks such as connectance, network specialisation $H_2'$ (a measure of specialisation at the network level, representing the assemblage of species and their interaction partners) and number of links per species, were determined using the "networklevel" function (see Blüthgen et al., 2006).

I tested if flower visitation (total flowers visited/tree species) depends on sunbird species (i.e. if sunbird species differed in their visitation rates to different tree species) using a one way

ANOVA. Flower visitation was the dependent variable with sunbird species as a fixed effects (predictors). I tested for normality using histograms and Q-Q plots. Levene's test was used to test the assumption for homogeneity of variance. Preliminary analysis on untransformed residuals suggests deviations from normality, so I square root transformed the data. I generated unstandardized residuals from the resulting transformed data, which were tested for normality. The residuals were normally distributed. However, the residuals did not conform to the assumption of homogeneity of variance ($p = 0.00$), suggesting a significant deviation from the assumption. To remedy this violation, I tested for a mean difference in flower visitation frequency of sunbird species using Welch statistics instead of the basic F statistics of the one-way ANOVA. Welch statistics is more robust to violation of assumption of equal variances and is therefore preferable to the F statistics when the assumption of equal variances does not hold. (Green & Salkind, 2003; SPSS one-way ANOVA help menu, SPSS version 15.0).

I used a linear mixed effects model ANOVA to test if sunbird species differed in the quantity of pollen they transported. To do this, the residuals generated from the linear mixed effect ANOVA model were tested to check for any violations of the assumption for parametric tests (i.e. normal distribution and equal variance).

A Q-Q plot revealed a marked deviation of the untransformed residuals from the linear fit expected under a normal distribution. To achieve normality, the data were square root transformed and an additional Q-Q plot of these transformed residuals confirmed that they were now normally distributed. The assumption of equal variances was also met (Levene's test, $p = 0.33$).

I then performed a linear mixed effects model ANOVA to determine whether sunbird species differed in the amount of pollen they transported. In the model, quantity of pollen transported was the dependent variable while sunbird species and tree species were the independent variables. Sunbird species was the fixed factor with eight levels (variable, orange tufted, green headed, northern –double collared, splendid, green, olive-bellied, and olive sunbird). To control for the problem of independence caused by including pollen load transported from the same bird species from all nine tree species, tree species was considered a random factor with nine levels (*N. congesta, A.noldeae, A. vogelii, D. ledermannii, A. gummifera, L. camara*, Mistletoe sp., Red vine, and unknown pollen).

There was a significant difference in quantity of pollen transported by different sunbird species ($F_{7, 19} = 3.304$, $p = 0.018$). Similarly, there was a significant difference in the quantity of pollen transported from the different plant species ($F_{8, 19} = 4.349$, $p = 0.004$).

To test for a relationship between the flower visitation and the pollen transport networks, I performed a Mantel test. Instead, I used an equivalent correlation coefficient "r" known as the standardized mantel statistics. "r" ranges from -1 to 1 and measures the strength of the relationship (with 1 implying a strong positive relationship and -1 a strong negative relationship).

I used the "Mantel.rtest" function in package "ade4" in R statistical software. Matrix entries were first converted to distance measures. I used a Monte Carlo test based on 10,000 random permutations. To generate a p-value, I calculated the correlation of the matrix entries, then permuted the matrices and calculated the same test statistics under each permutation.

Most analyses were carried out using R (R statistical software, version 2.15.3, R development core team, 2013). Univariate analysis, correlation analysis and graphical explorations were done using IBM SPSS version 21.0 (IBM Corp, 2012).

### 3.2.1: Nestedness and Null model formulation

In order to determine the significance of nestedness and to ascertain that values of nestedness were not products of chance, a null model approach was followed. A null model is a pattern-generating model that is based on randomisation of ecological data from a known or imagined distribution (Gotelli & Graves, 1996, pg 3). Since nestedness is believed to increase with complexity (i.e. network dimension: number of animal and tree species) (Bascompte et al., 2003; Dormann et al., 2009), null models designed to compare structural differences between networks maintain the original dimension of the observed network and randomises the position or interactions between species based on their degree (i.e. the number of links).

In my null model, the new networks were randomly created using the same dimensions and number of realised links as the observed networks (Bascompte et al., 2003).

The model was designed to allow for equal probability of cell occupancy or interactions (that is, the model controlled for a species' degree and relative abundance). Hence, in my model, each cell in the matrix had an equal probability of being filled. This model is based on null model 1 (shuffle.web algorithm) in Bascompte et al. (2003). See (Appendix 3.5) for details of the null model equation.

For both visitation and pollen transport networks, I randomly generated 1,000 matrices. I obtained a mean value of the NODF scores from the 1,000 matrices, and compared the mean NODF values with those of the observed nestedness score. I evaluated the level of deviation of the null model outcome of nestedness from the observed. ~~Z~~ statistics were used to determine if their deviation was significant. For each network (FVN and PTN), I hypothesised that observed networks were significantly more nested than randomised networks.

**Network Specialisation**

I used the index $H_2'$ - a measure of specialisation at the network level, representing the assemblage of species and their interaction partners. $H_2'$ was used in comparing both networks because it is invariant to network dimension, network architecture or total number of interactions and thus very suitable for comparing matrices of a different scale (Blüthgen et al., 2006).

**Species composition**

Both networks were analysed to determine differences and/or similarities in the species composition, using the Jaccard similarity index. The Jaccard index is a statistic used for comparing the similarity and diversity of sample sets (e.g. similarities in species assemblage across networks) and was very appropriate for this study.

The formula for this index is:

$$C_j = \frac{a}{(a+b+c)} \quad . \qquad \text{Equation 3.1}$$

Where $C_J$ = Jaccard index or coefficient of similarity, $a$ = number of species found in both samples (networks). $b$ and $c$ are two sample sets (networks); $b$ represents number of species found in sample $b$ and not $c$ (i.e. species unique to $b$), while $c$ represents number of species found in $c$ and not in $b$ (i.e. species unique to $c$). Jaccard similarity index ranges from 0 when no links are shared to 1 when the samples are identical.

I used the Jaccard similarity index to estimate how well each structure or matrix reflects the other. Jaccard index compares the similarity and diversity of sample sets, and is the value obtained when the size of the intersection is divided by the size of the union of two sample sets (in this case two interaction networks).

### 3.2.2: Hypotheses testing:

i) Flower visitation networks are a good reflection of pollen transport networks so that birds that visit flowers the most will also transport the most pollen.

I tested this hypothesis using a Mantel test.

ii) The tree species composition in the pollen transport network (PTN) will be similar in species composition to those of tree species in the flower visitation network (FVN).

I tested this hypothesis by determining if the Jaccard similarity index between the two networks was > 0 or = 1.

iii) There will be no difference in flower visitation frequency and quantity of pollen transported among sunbird species, and therefore the visitation and pollination networks will be symmetrical.

I used Analysis of variance (see section 3.2) to test for differences in visitation frequencies among sunbird species and the variation in pollen transport efficiencies among sunbird species..

iv) The observed NODF values for FVN and PTN would be similar with those obtained from 1000 randomised matrices of each of the observed networks.

Z statistics were used to test for differences in observed NODF for FVN and PTN and the null model expectation (mean NODF).

## 3.3: Results

A total of 16 tree species were found during field assessment and were observed. Of these 16 flowering tree species, 14 tree species were visited by sunbird species during flower visitation observation (Appendix 3.2). Seven out of ten species of sunbirds were recorded during flower visitation observation, five of which were also captured in mist nets; with an additional three species (green sunbird *Anthrepetes rectirostris*, olive sunbird *Cyanomitra olivaceus* and olive bellied sunbird *Cinnyris chloropygius*) recorded exclusively as captures during mist netting, making a total of ten species of sunbirds in all (Appendix 3.3). One species, pygmy sunbird *Anthodiaeta platura* was never captured or observed on the flowers of any tree species although it was recorded in one of the fragments during transect survey. Sunbirds visited tree species a total of 2,393 times and contacted 26,244 flowers of 70 individuals of 14 tree species; after a total of 1680 mins (28 hrs) of focal observation

### 3.3.1: Flower Visitation and Pollen transport

#### Visitation

Sunbird species differed in the frequency of visits they made to various tree species ($F_{6, 7.2} = 4.26$, $p = 0.03$). On average most species from the genus *Cinnyris* visited and contacted the flowers of tree species more frequently than species in less common genera such as *Cyanomitra* and *Hedydipna* (Appendix 3.7). Some tree species such as (*Newtonia buchananni* and *Deinbolia pinnata*) were never visited by a single sunbird species throughout the observation period and have been excluded in all analyses (Appendix 3.2).

#### Pollen transport

There was a significant difference in quantity of pollen transported by different sunbird species ($F_{7, 19} = 3.304$, $p = 0.018$). Similarly, there was a significant difference in the quantity of pollen transported from the different plant species ($F_{8, 19} = 4.349$, $p = 0.004$). Species in the genus *Cyanomitra* transported more pollen on average than species in the genus *Cinnyris* (Appendix 3.6).

### 3.3.2 Network level analysis.

Bipartite analyses showed a 14 (tree species) x seven (sunbird species) and nine (tree species) x eight (sunbird species) bipartite structures for flower visitation and pollen transport networks respectively.

**Similarity in species composition between the two networks**

The Jaccard index of similarity between the two networks (Appendix 3.1) = 0.36, which implies that there was a 36 % similarity in species composition between the flower visitation and the pollen transport networks. Eleven and seven species (i.e. both bird and tree species) were unique to the flower visitation and pollen transport networks respectively. The Collared sunbird *Hedydipna collaris* and Copper sunbird *Cinnyris cupreus* were unique to the FVN. The Olive sunbird, Olive -bellied sunbird and Green Sunbird were unique to the PTN.

The flower visitation network had five tree species more than the pollen transport network, which accounted for the greater number of interaction links per sunbird species in this network (Table 3.2).

**Nestedness:**

Both the flower visitation and pollen transport networks were nested (Table 3.1). The value of nestedness (NODF = 88.88) for the pollen transport network was more than the flower visitation network (NODF = 73.23) (Table 1). Both these empirical values of nestedness were significantly higher than the mean NODF score derived from the Null model (Table 3.1), ~~Z~~ = 4.37, $P < 0.005$ (flower visitation network) and ~~Z~~ = 7.4, $P < 0.005$ pollen transport networks.

Table 3.1: Summary of null model analysis of nestedness for flower visitation and pollen transport Networks. Randomised NODF = mean of NODF obtained from 1000 randomised matrices.

| Networks | Observed NODF | Randomised NODF | Standard Deviation | Z score | P-value |
|---|---|---|---|---|---|
| Flower visitation | 73.23 | 49.68 | 5.38 | 4.37 | 0.005 |
| Pollen transport | 88.88 | 43.94 | 6.07 | 7.4 | 0.005 |

Table 3.2: Summary of network level analysis showing some key properties of two mutualistic networks a) Flower visitation network (FVN) and b) pollen transport network (PTN). These particular properties were included because they respond differently to first-order properties of network. $H_2'$ is invariant to network size, hence a good index for a comparison of networks of different dimensions. Connectance and links/species reflects first-order properties of network such as abundance and degree (number of links or partners).

| Parameters | FVN | PTN |
|---|---|---|
| Sunbird species | 7 | 8 |
| Plant species | 14 | 9 |
| Connectance | 0.52 | 0.45 |
| Links/species | 2.43 | 1.94 |
| $H_2'$ (specialisation) | 0.13 | 0.21 |

### 3.3.3: Relationship between the pollen transport and flower visitation networks

Based on Monte- Carlo randomization, the standardized Mantel statistics (i.e. observed correlation), r = 0.74, suggests that the matrix entries (i.e. the FVN and PTN) are positively associated. This association although highly positive, was not significant, p = 0.08.

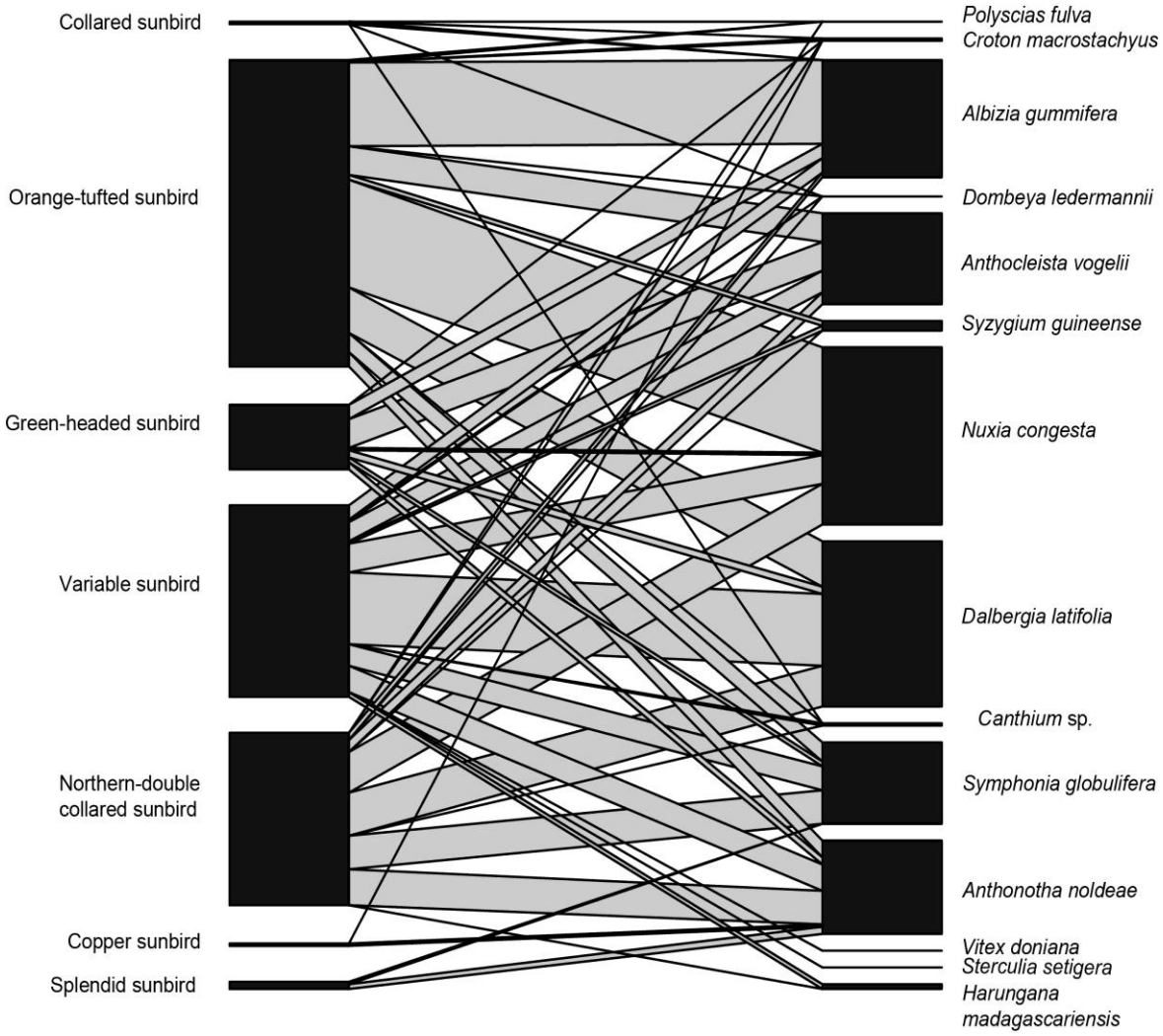



Figure 3.3: Flower visitation network structure. Counts reflect the frequency of flowers contacted by sunbird species per tree species. In this web, the size of the black bars on the right represents the proportion of flowers visited by the bird species. The length of the left bar represents the relative abundance of bird species, while the width of the bar linking the sunbird species and plant species represents the frequency of interaction.

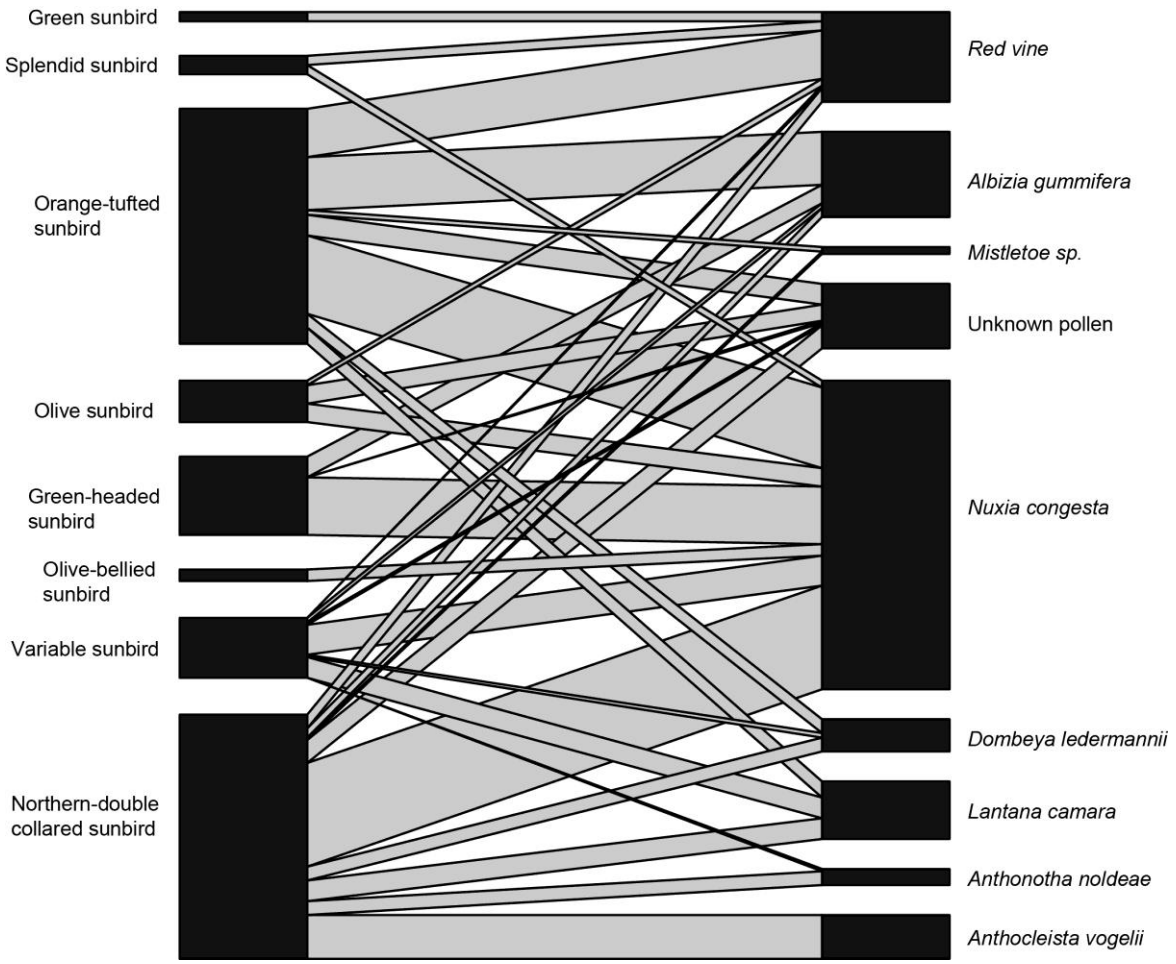



Figure 3.4: Pollen transport network structure. Counts were made on the quantity of pollen (no. of grains transported by sunbird species per tree species). In this web, the size of the black bars on the left represents the relative abundance of sunbird species, while that of the right bars represents the cumulative amount of pollen transported by individuals of each sunbird species. The width of the bar linking the sunbird species and plant species represents the frequency of the interaction. Notice the difference in tree species composition between the FVN (Figure 3.3) and PTN web. The PTN is almost a sub-set of the FVN due to some shared tree species, but the fact that PTN has some unique species illustrates that the FVN is not a complete reflection of the PTN.

## 3.4: Discussion

In this study, I investigated whether a sunbird-tree pollination network corresponds to a sunbird-tree visitation *network?* To answer this question, I combined two approaches. Firstly, I compared the structure of the two networks and secondly, I determined the congruence between the networks in terms of the proxy for pollination effectiveness, I used (pollen transport); I determined whether frequent flower visitors were also the most efficient transporters of pollen.

**Species composition approach**

The two networks shared 36% of their species. This is very surprising considering the strong positive correlation between the FVN and PTN. The 64 % dissimilarity in species composition can be explained primarily by the differences in sizes of the network. It is expected that networks that differ in dimension would be poor mirror reflections of each other.

Our results must be interpreted with caution because there are important logistic constraints with observing pollination at our field site. Observations of some flowers were difficult resulting in limitations of the FVN. Some tree species grew in difficult to access parts of our field site; some were not observable from the ground, while others may have flowered during parts of the year when observation was difficult. In contrast, the PTN was limited not by choice of plant species but by time. Pollen extraction from the bodies of trapped sunbird species revealed pollen from non target species (non-tree species) such as *Mistletoe* sp. *Lantana camara,* an un-identified vine species and about 10 % from various unidentified sources, categorized here as unknown pollen. As can be seen in this study the FVN was short of representing the actual or complete realised interactions in the PTN and therefore only a subset of the actual pollination network from the bird's perspective (see Dorado et al., 2011).

This result suggests that trees that are linked by visitation may have potentially different interactions from those that are linked by pollen transport (pollination) (Popic et al., 2013).

**Nestedness**

I found that the FVN had more nodes than the PTN (Figure 3.3 and 3.4, and was less nested than the PTN even if there were relatively minor differences in nestedness (73.23 and 88.88) for FVN and PTN respectively. The fact that the FVN was less nested than the PTN may best be explained by the dimension of the networks (i.e. number of sunbird and tree species) (Dorman et al., 2009). Many networks have more animal than plant species. This was the case with PTN but not the FVN in this study (see Bascompte et al., 2003; Dorman et al., 2009). The unusual pattern in FVN could be due to my focus on a particular taxon (sunbirds), with a finite diversity/distribution.

I found more nestedness than we would expect by chance. The little difference in nestedness observed between these networks (FVN and PTN) despite differences in network size (number of partners in each bipartite group) and abundance (weighted frequency of flower visited and pollen load) (Figure 3.3 and 3.4), suggest that nestedness explains network structure beyond what is reflected by other network properties such as connectance, links per species etc.

Although nestedness differed significantly between observed and randomised matrices for flower and pollen networks, the numerical difference in the value of nestedness (Table 3.1) was more pronounced for PTN than for FVN respectively. The small margin of difference in NODF value between observed and randomised matrices for FVN compared to that of PTN could be an indication that some of the interactions might have been random. The intuition that FVN structure is partly mediated by chance is because birds visit flowers for various reasons: to hunt for insects, rob nectar, collect pollen or eat petals. These interactions vary

from time to time, and would definitely reduce or mute the causal effect of any single biological process; making it more plausible to attribute some of the interactions, hence part of the structure to chance. On the contrary, the interaction that defines PTN is basic and more predictable; since pollen movement or displacement is more likely to occur after a bird contacts a flower. However, the significant difference between observed nestedness of FVN and null should be seen as a caveat, that attributing structural patterns resulting from FVN to a particular causal factor or mechanism should be an exception not a rule. This view has also been suggested elsewhere (Mcquaid & Britton, 2013).

Overall, the relatively high values of nestedness obtained for both networks is in agreement with previous empirical studies that have shown plant pollinator networks to be generally highly nested (Bascompte et al., 2003). The relatively high level of nestedness and low level of specialisation observed in this study (Table 3.2) is of ecological significance. It implies that: species (sunbird and trees), have a high survival probability due to the possibility of alternative partners, especially in the event of any loss in species due to some stochastic disturbance. Naturally, generalist species are more prone to coexist with new species, as this would offer more opportunity for partnership; whereas, a specialised interaction structure would naturally provide less opportunity for coexistence and integration of new species (Dorado et al., 2011). Therefore, the generalised pollination (flower visitation and pollen transport) interaction networks imply that there is potential for growth and expansion through addition of new species (both trees and birds) to the existing sunbird-tree community at Ngel Nyaki forest.

**Other network descriptors (connectance, links per species and $H_2'$)**

In my study, there was little difference between the visitation and transportation networks in the number of links per species or $H_2'$ (specialisation) (Table 3.2). The observed similarity appears to contradict major differences in species composition. Emphasis ought to be on species. Species are the key elements that determine network structure, analogous to bricks in a building. Future studies comparing networks, should therefore, in addition to evaluating network structure, consider the similarities in species assemblage between networks especially those occurring in different geographical regions or separated in space and time, as this may foster understanding of co-evolutionary forces shaping species interaction and network structure.

**Functional similarity**

Functionally, the level of similarity between the flower visitation and pollen transport networks could be explained by the fact that most species that were active as frequent flower visitors were also active as pollen transporters. This is probably why we found a positive relationship between the flower visitation and the pollen transport network, despite a 64 % structural dissimilarity. The positive correlation is also explained by the number of shared pollinators and host. However, in terms of specialisation, the pollen transport network was found to be more specialised than the flower visitation network. The higher level of specialisation of PTN relative to FVN (Table 3.2) has also been reported elsewhere in similar studies (Alarcon, 2010; Popic et al., 2013).

**Species flower visitation and pollen transport efficiencies: implications for the efficacy of network proxies.**

Our results show that sunbird species differed in their visitation rates and in the amount of pollen they transported. For instance, species from the genus *Cyanomitra* (green- headed sunbird *C, verticalis* and olive sunbird *C. olivaceus*) transported more pollen on average than most members of the *Cinnyris* genus, while those from the genus *Cinnyris* were more active or "efficient" as flower visitors. Nevertheless, in terms of overall contribution, the relatively high frequency of visitation of members in the genus *Cinnyris*, (Orange-tufted sunbird *C. bouveri,* Northern-double collared sunbird *C. reichenowi,* and Variable sunbird *C. venustus*), (Appendix 3.2 and 3.7) may compensate for their relatively lower contributions with regards to quantity of pollen transported; however, this balance may be at the expense of the tree species if it turns out that the sunbird species in question (members of the genus *Cinnyris*) are pollen wasters, also considering the fact that they are relatively very abundant, but see Vazquez et al. (2005), Vazquez et al. (2012).

The above findings highlight the benefits of a holistic approach in assessing species efficiency and functional properties of interaction networks. Based on pollen transport, the less common species (*C. verticalis* and *C. olivaceus*) in the genus *Cyanomitra* would be considered more efficient than species from other genera, while an assessment based on frequency of visitation would bias members of this genus (*Cyanomitra*). Likewise, the variable sunbird a member of the genus *Cinnyris* and the second most frequent flower visitor would have been undervalued as a pollinator if assessment was only based on pollen transportation. Most importantly, three bird species, green sunbird**,** olive sunbird, olive-bellied sunbird would have been excluded from the sunbird tree pollination network had I limited my assessment to just flower visitation. This finding demonstrates that reliance on flower visitation alone may be inadequate for describing pollination systems and when evaluating the relative effectiveness of avian pollinators and in fact, other biotic agents.

The results of my study, as in other studies (Vázquez et al., 2012; Vázquez et al., 2005) found that flower visitation frequency is positively correlated with species abundance and is a good proxy for assessing the efficiencies of pollinators. At Ngel Nyaki, members of the genus *Cinnyris* are the most common and abundant sunbird species and are responsible for about 85 % of flower visitations to three most abundant bird-visited tree species at the reserve (Nsor & Chapman, 2013). In contrast, members of the genus *Cyanomitra* are relatively scarce and limited in their distribution. However, my results indicate that though some species may be too rare to qualify as frequent visitors, they are actually important in the PTN architecture. For example in my study, species of *Cinnyris* are very important pollinators and as such are major contributors to the PTN architecture. This is clear in Figures 3.3 and 3.4 which illustrate that members of this genus were the main links in the FVN and PTN networks and were almost all common to both networks. Therefore, members of this genus could be key determinants of community stability (i.e. the ability to withstand disturbance without collapse) at Ngel Nyaki forest reserve. On the other hand it is possible that the observed trend and perceived rarity (reflected in low relative abundance) for members of the genus *Cyanomitra* and some species that were singleton observations like green sunbird could be due to sampling artefact. The conclusions made here are therefore guarded by the obvious limitations of sample size and effort (Dorado et al., 2011).

Furthermore, the structures of both pollen transport and flower visitation networks are merely "snap shots" in space and time (Lawton, 1990), and only capture the topological dynamics of the network for the period under consideration. This is because, most sunbird species are seasonal migrants, and flowering phenology is highly seasonal. Times of year of assessment, duration of observation or experimentation are also key factors to be considered. This is especially so for some network indices that are sensitive to first order network properties such

as abundance and degree (See Blüthgen et al., 2006). While I have identified space and time as possible limitations to the application or implication of these network structures on a broad scale, it is also important to consider that most webs naturally occur in a spatial framework with the potentials for active linkages across systems (Menge, 2000; Polis et al., 1997).

**Additional limitations**

I have assumed that the PTN is a true description of the "pollination system" or network. However, I have not proven this. For a true pollination network it would be necessary to identify whether or not the pollen transported by sunbird species gets delivered to an appropriate and compatible stigma, and further, confirm that the fertilized ovule matures into a healthy seed.

My method of estimating pollen load through mist-netting assumed that the amount of pollen extracted from the bodies of sunbird species was a reflection of the full load "total amount per capture." However, the quantity of pollen presented here is most likely a fraction of what was actually transported by the sunbird species, since some of the pollen grains would have been lost in the course of extracting the birds from the nets. Future work focusing on birds should explore other ways of ensuring that flowers that are visited by sunbirds are monitored until fruit or seed-set through exclusion experiments. This approach would complement information derived from pollen extraction thereby validating any conclusions on the efficiencies and level of specialisation of sunbird species or pollinators. Additional effort should be made to capture as many rare species as possible to reduce the likelihood of conclusions that could be liable to a "type 1 or type II error".

While it seems that the two networks were structurally different by default, I must draw attention to the fact that methodological constraints also contributed to the differences. For instance, the composition of the pollen network was largely determined by the sunbird

species at random (i.e. through the various tree species pollen they transported), while the flower network on the other hand was predetermined by experimental design.

### 3.5: Conclusion

Although structurally similar, the observed dissimilarities in species assemblage and function between the pollen transport and flower visitation networks indicate that first-order approximation of pollination systems using flower visitation networks alone is inappropriate and rather misleading. My approach of combining the flower visitation and pollen transport networks is a more robust approach to determining the pollination efficiencies in our community.

Because species abundance and diversity control most secondary properties of networks such as connectance, number of links per species and to some extent nestedness, they are the main determinants of network structure. Therefore, most abundant species in the sunbird-tree networks in this thesis, which are from the genus *Cinnyris* are the most crucial for network structure. Exclusion of members of this genus from the network will definitely alter the topology (structure) of the present networks or dislodge the existing links. Finally, based on the level of specialisation and nestedness obtained from my analysis, the Ngel Nyaki sunbird-tree pollination network would most likely support species addition to the existing network and by extension more biodiversity.

# APPENDICES

Appendix 3.1: Species assemblage (presence (1) and absence (0)) in the flower visitation and pollen transport networks.

| S/N | Species | Flower Visitation | Pollen Transport | Trophic level |
|---|---|---|---|---|
| 1 | Orange tufted sunbird | 1 | 1 | Upper |
| 2 | Northern-double collared | 1 | 1 | Upper |
| 3 | Variable sunbird | 1 | 1 | Upper |
| 4 | Green-headed sunbird | 1 | 1 | Upper |
| 5 | Collared sunbird | 1 | 0 | Upper |
| 6 | Splendid sunbird | 1 | 1 | Upper |
| 7 | Copper sunbird | 1 | 0 | Upper |
| 8 | Olive-bellied sunbird | 0 | 1 | Upper |
| 9 | Olive sunbird | 0 | 1 | Upper |
| 10 | Green sunbird | 0 | 1 | Upper |
| 11 | Albizia gummifera | 1 | 1 | lower |
| 12 | Nuxia congesta | 1 | 1 | lower |
| 13 | Syzygium guineense | 1 | 0 | lower |
| 14 | Dombeya ledermannii | 1 | 1 | lower |
| 15 | Canthium sp. | 1 | 0 | lower |
| 16 | Polyscias fulva | 1 | 0 | lower |
| 17 | Anthocleista vogelii | 1 | 1 | lower |
| 18 | Dalbergia sp. | 1 | 0 | lower |
| 19 | Anthonotha noldeae | 1 | 1 | lower |
| 20 | Harungana madagascariensis | 1 | 0 | lower |
| 21 | Symphonia globulifera | 1 | 0 | lower |
| 22 | Croton macrostachyus | 1 | 0 | lower |
| 23 | Vitex doniana | 1 | 0 | lower |
| 24 | Sterculia setigera | 1 | 0 | lower |
| 25 | Unknown | 0 | 1 | lower |
| 26 | Lantana camara | 0 | 1 | lower |
| 27 | Mistletoe sp. | 0 | 1 | lower |
| 28 | Red vine. | 0 | 1 | lower |
| | **Total species** | **21** | **17** | |

Jacccard index of similarity was calculated using the equation: $C_J = a/(a + b + c)$

Where $C_J$ = Jaccard index or coefficient of similarity, $a$ = number of species found in both samples (networks). $b$ and $c$ are two sample sets (networks), $b$ represents number of species found in sample $b$ and not $c$ (i.e. species unique to $b$), while $c$ represents number of species found in $c$ and not in $b$ (i.e. species unique to $c$). Jaccard similarity index ranges from 0 when no links are shared to 1 when the samples are identical.

$$C_j = \frac{a}{(a + b + c)}$$

= 10/(10 + 11 + 7) = 10/28 = **0.357**.

Appendix 3.2: Summary of flower contact/visitation frequency of sunbird species and tree species during 120 minutes of focal observation. Bird and tree species appear on first row and column, respectively. Cell values correspond to total number of flowers contacted per total visit.

| S/N | SPECIES | OTSB | NDSB | VSBD | GHSB | CLSB | SPSB | COSB |
|---|---|---|---|---|---|---|---|---|
| 1 | Albizia gummifera | 2903 | 214 | 505 | 535 | 58 | 0 | 0 |
| 2 | Nuxia congesta | 3746 | 1469 | 957 | 74 | 0 | 0 | 0 |
| 3 | Syzygium guineense | 202 | 22 | 114 | 0 | 0 | 0 | 0 |
| 4 | Dombeya ledermannii | 10 | 4 | 14 | 0 | 7 | 0 | 0 |
| 5 | Canthium sp. | 5 | 25 | 12 | 0 | 4 | 0 | 0 |
| 6 | Polyscias fulva | 8 | 1 | 0 | 0 | 1 | 0 | 0 |
| 7 | Anthocleista vogelii | 1028 | 406 | 711 | 1019 | 0 | 0 | 0 |
| 8 | Dalbergia sp. | 1597 | 1465 | 2547 | 215 | 0 | 0 | 0 |
| 9 | Anthonotha noldeae | 562 | 1235 | 919 | 235 | 0 | 212 | 60 |
| 10 | Harungana madagascariensis | 0 | 24 | 113 | 0 | 0 | 0 | 0 |
| 11 | Symphonia globulifera | 681 | 1213 | 788 | 182 | 0 | 34 | 0 |
| 12 | Croton macrostachyus | 68 | 6 | 0 | 7 | 1 | 0 | 3 |
| 13 | Vitex doniana | 0 | 0 | 13 | 0 | 0 | 0 | 0 |
| 14 | Sterculia setigera | 0 | 0 | 10 | 0 | 0 | 0 | 0 |
| 15 | Newtonia buchananii | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 16 | Deibolia pinnata | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

Appendix 3.3: Sunbird species diversity at Ngel Nyaki Forest reserve at the time of the various assessments.

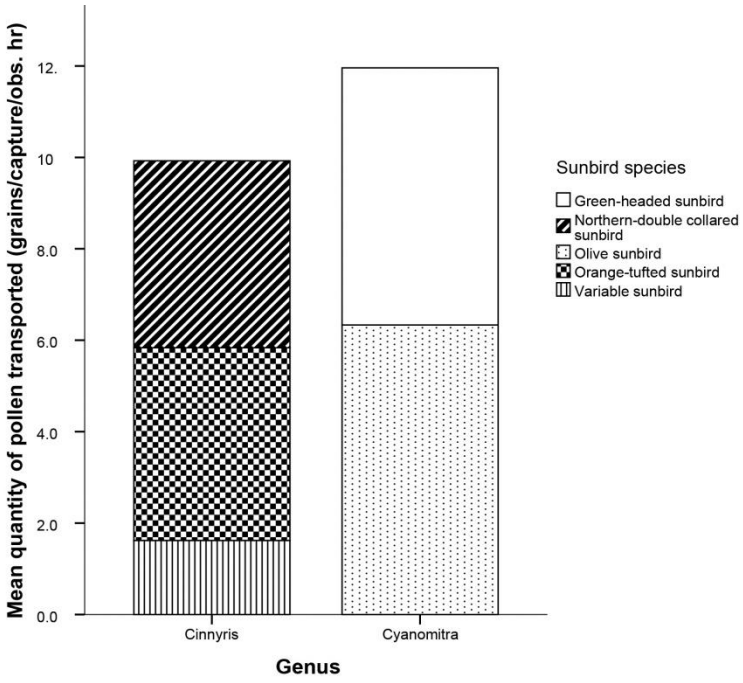
| S/N | SPECIES | SCIENTIFIC NAME | GENUS | LOCAL STATUS | COUNTRY STATUS |
|---|---|---|---|---|---|
| 1 | Olive Sunbird | Cyanomitra olivaceus | Cyanomitra | Resident but uncommon | Common resident |
| 2 | Collared Sunbird | Hedydipna collaris | Hedydipna | Resident but uncommon | Common Resident |
| 3 | Green-headed Sunbird | Cyanomitra verticalis | Cyanomitra | Resident but uncommon | Common resident |
| 4 | Variable Sunbird | Cinnyris venustrus | Cinnyris | Resident and partial migrant | Common resident, partially migratory |
| 5 | Olive bellied Sunbird | Cinnyris chloropygius | Cinnyris | Partial migrant | Common resident, partially migratory |
| 6 | Northern Double | Cinnyris reichenowi | Cinnyris | Most common resident | Range-restricted |
| 7 | Orange tufted Sunbird | Cinnyris bouvieri | Cinnyris | Very common resident | Range restricted |
| 8 | Copper Sunbird | Cinnyris cupreus | Cinnyris | Uncommon resident | Common resident |
| 9 | Splendid Sunbird | Cinnyris coccinigastrus | Cinnyris | Uncommon resident | Common resident |
| 10 | Green Sunbird | Anthreptes rectirostris | Anthreptes | Uncommon resident | New in range |

Appendix 3.4: Taxonomy and distribution status of tree species observed at Ngel Nyaki

| S/n | Species | Family | Distribution status | Habitat | IUCN status |
|---|---|---|---|---|---|
| 1 | Deinbollia pinnata | Sapindaceae | Common | Forest edge/fragment | LC |
| 2 | Harungana madagascariensis | Hypericaceae | Not common | Forest core | LC |
| 3 | Anthonotha noldeae | Leguminaceae | Common | Forest edge | LC |
| 4 | Anthocleista vogelii | Gentianaceae | Common | Riparian Fragment | LC |
| 5 | Croton macrostachyus | Euphorbiaceae | Common | Riparian fragment | LC |
| 6 | Nuxia congesta | Loganiaceae | Common | Forest edge/ fragment | LC |
| 7 | Albizia gummifera | Fabaceae | Common | Riparian Fragments | LC |
| 8 | Newtonia buchananii | Fabaceae | Common | Forest edge | LC |
| 9 | Syzygium guineense | Myrtaceae | Common | Riparian Fragment | LC |
| 10 | Dombeya ledermannii | Sterculiaceae | Common | Forest edge | CR |
| 11 | Canthium sp. | Rubiaceae | Common | Forest edge | LC |
| 12 | Dalbergia sp. | Fabaceae | Common | Forest edge | VU |
| 13 | Polyscias fulva. | Araliaceae | Common | Forest edge/Fragment | LC |
| 14 | Symphonia globulifera | Clusiaceae | Common | Forest edge | LC |
| 15 | Vitex doniana | Verbanaceae | Common | Forest edge | LC |
| 16 | Sterculia setigera | Malvaceae | Common | Forest edge | LC |

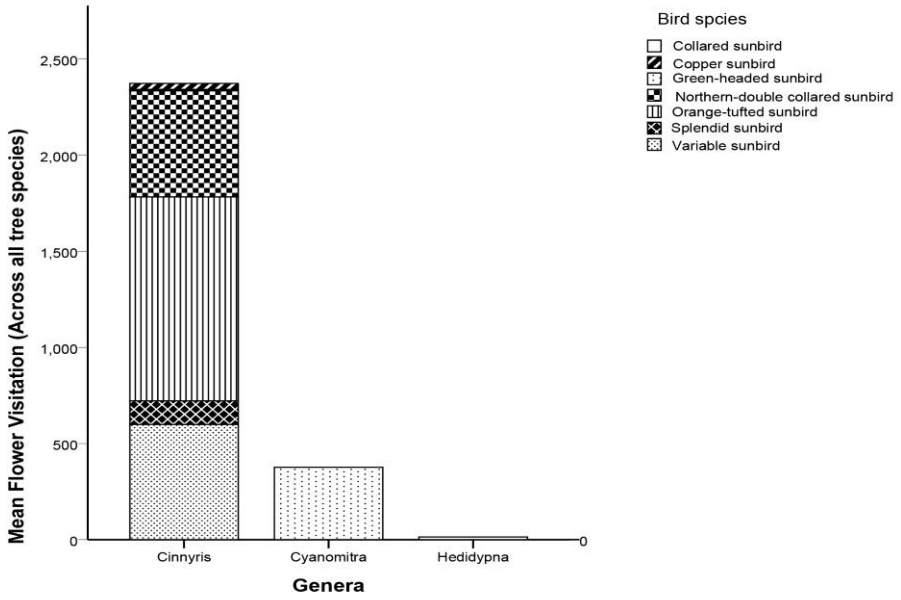
Appendix 3.5: Quantity of pollen of various tree species removed from the body of captured sunbird species. Sunbird species are listed at the top row while tree species are on the second column.

| S/N | SPECIES | OTSB | NDSB | VSBD | GHSB | SPSB | OBSB | OLSB | GRSB |
|---|---|---|---|---|---|---|---|---|---|
| 1 | Albizia gummifera | 31 | 6 | 2 | 11 | 0 | 0 | 0 | 0 |
| 2 | Nuxia congesta | 46 | 60 | 18 | 33 | 5 | 7 | 11 | 0 |
| 3 | Dombeya ledermannii | 8 | 8 | 2 | 0 | 0 | 0 | 0 | 0 |
| 4 | Anthocleista vogelii | 0 | 25 | 0 | 0 | 0 | 0 | 0 | 0 |
| 5 | Anthonotha noldeae | 0 | 8 | 1 | 0 | 0 | 0 | 0 | 0 |
| 6 | Unknown pollen | 2 | 12 | 1 | 1 | 0 | 0 | 6 | 0 |
| 7 | Lantana camara | 1 | 11 | 9 | 0 | 0 | 0 | 0 | 0 |
| 8 | Mistletoe sp. | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 9 | Red vine | 7 | 8 | 1 | 0 | 6 | 0 | 2 | 5 |




Appendix 3.6: Variation in mean quantity of pollen obtained from trapped sunbird species at Ngel Nyaki Forest Reserve. Variation was also observed within and between generic groups. Bird species with N < 3 individuals were excluded from the analysis. Species are

differenciated by pattern of segment fill. Each bar represents the mean amount of pollen transported by genus.




Appendix 3.7: Variation in mean flower visitation frequency of sunbird species and genera. Each bar represents the mean visitation frequency of each genus; while bar segments represent each species. Species are differentiated by pattern of segment fill.

## REFERENCES


Alarcón, R. (2010). Congruence between visitation and pollen-transport networks in a California plant–pollinator community. *Oikos*, 119(1), 35-44.

Alarcón, R., Waser, N. M., & Ollerton, J. (2008). Year-to-Year Variation in the Topology of a Plant-Pollinator Interaction Network. *Oikos*, 117(12), 1796-1807.

Almeida-Neto, M., Guimaraes, P., Guimarães, P. R., Loyola, R. D., & Ulrich, W. (2008). A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos*, 117(8), 1227-1239.

Araujo, A. I. L., de Almeida, A. M., Cardoso, M. Z., & Corso, G. (2010). Abundance and nestedness in interaction networks. *Ecological Complexity*, 7(4), 494-499.

Atmar, W., & Patterson, B. D. (1993). The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia*, 96(3), 373-382.

Bascompte, J., Jordano, P., Melián, C. J., & Olesen, J. M. (2003). The Nested Assembly of Plant-Animal Mutualistic Networks. *Proceedings of the National Academy of Sciences of the United States of America*, 100(16), 9383-9387.

BirdLife International. (2013). *State of the World's Birds*: Indicators for our changing world. Cambridge, UK, BirdLife International, Pg 9.

Blüthgen, N., Menzel, F., & Blüthgen, N. (2006). Measuring specialisation in species interaction networks. *BMC ecology*, 6(1), 9.

Borrow, N., & Demey, R. (2001). *A Guide to the Birds of Western Africa*. Princeton University Press.

Brualdi, R. A., & Sanderson, J. G. (1999). Nested species subsets, gaps, and discrepancy. *Oecologia*, 119(2), 256-264.

Chapman, J. D., & Chapman, H. M. (2001) *The Forests of Taraba and Adamawa States, Nigeria. An Ecological Account and Plant Species Checklist*. University of Canterbury, Christchurch, New Zealand.

Dorado, J., Vázquez, D. P., Stevani, E. L., & Chacoff, N. P. (2011). Rareness and specialisation in plant-pollinator networks. *Ecology*, 92(1), 19-25.

Dormann, C. F., Fründ, J., Blüthgen, N., & Gruber, B. (2009). *Indices, Graphs and Null Models*: analysing bipartite ecological networks.

Dowsett-Lemaire, F. (1989). Physiography and vegetation of the highland forests of eastern Nigeria. A preliminary natural history survey of Mambilla Plateau and some lowland forests of eastern Nigeria. Ely, Tauraco Press (*Tauraca Research Report*, 1), 6-12.

Fishpool, L. D., & Evans, M. I. (2001). *Important Bird Areas in Africa and Associated Islands*: Priority sites for conservation. BirdLife International Cambridge, UK.

Fleishman, E., Donnelly, R., Fay, J. P., & Reeves, R. (2007). Applications of nestedness analyses to biodiversity conservation in developing landscapes. *Landscape and Urban Planning*, 81(4), 271-281.

Fortuna, M. A., & Bascompte, J. (2006). Habitat loss and the structure of plant–animal mutualistic networks. *Ecology Letters*, 9(3), 281-286.

Forup, M. L., Henson, K. S. E., Craze, P. G., Memmott, J., & Memmot, J. (2008). The Restoration of Ecological Interactions: Plant-Pollinator Networks on Ancient and Restored Heathlands. *Journal of Applied Ecology*, 45(3), 742-752.

Gotelli, N. J., & Graves, G. R., (1996). *Null Models in Ecology*.

Green, S. B., Salkind, N. J., & Green, S. B. (2003). *Using SPSS for Windows and Macintosh: Analyzing and understanding data*. Upper Saddle River, N.J: Prentice Hall.

James, A., Pitchford, J. W., & Plank, M. J. (2012). Disentangling nestedness from models of ecological complexity. *Nature*, 487(7406), 227-230.

Jordano, P. (1987). Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. *The American naturalist*, 657-677.

Jordano, P., Bascompte, J., & Olesen, J. M. (2003). Invariant properties in coevolutionary networks of plant–animal interactions. *Ecology Letters*, 6(1), 69-81.

Kearns, C. A., & Inouye, D. W. (1993). *Techniques for Pollination Biologists*. University Press of Colorado.

King, C., Ballantyne, G., & Willmer, P. G. (2013). Why flower visitation is a poor proxy for pollination: measuring single-visit pollen deposition, with implications for pollination networks and conservation. *Methods in Ecology and Evolution*, 4(9), 811-818.

Lawton, J. (1990). Species richness and population dynamics of animal assemblages. Patterns in body size: abundance space. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 330(1257), 283-291.

Manu, S., Imong, I. S., & Cresswell, W. (2010). Bird species richness and diversity at montane Important Bird Area (IBA) sites in south-eastern Nigeria. *Bird Conservation International*, 20(3), 231-239.

McQuaid, C. F., & Britton, N. F. (2013). Coevolution of resource trade-offs driving species interactions in a host–parasite network: an exploratory model. *Theoretical Ecology*, 6(4), 443-456.

McQuaid, C. F., & Britton, N. F. (2013). Trophic Structure, Stability, and Parasite Persistence Threshold in Food Webs. *Bulletin of mathematical biology*, 75(11), 2196-2207.

Memmott, J. (1999). The structure of a plant-pollinator food web. *Ecology letters*, 2(5), 276-280.

Menge, B. A. (2000). Recruitment vs. postrecruitment processes as determinants of barnacle population abundance. *Ecological Monographs*, 70(2), 265-288.

Ne'eman, G., Jürgens, A., Newstrom-Lloyd, L., Potts, S. G., & Dafni, A. (2010). A framework for comparing pollinator performance: effectiveness and efficiency. *Biological Reviews*, 85(3), 435-451.

Nsor, C. A., & Chapman, H. M. (2013). A preliminary investigation into the avian pollinators of three tree species in a Nigerian Montane Forest. *Malimbus*, 35, 37-49.

Pellmyr, O., Herrera, C., & Pellmyr, O. (2002). Pollination by animals. *Plant–animal interactions, an evolutionary approach*, 157-184.

Polis, G. A., Anderson, W. B., & Holt, R. D. (1997). Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics*, 289-316.

Popic, T. J., Wardle, G. M., & Davila, Y. C. (2013). Flower-visitor networks only partially predict the function of pollen transport by bees. *Austral Ecology*, 38(1), 76-86.

R Core Team. (2013). R: *A language and Environment for Statistical Computing*. R Foundation for statistical Computing, Vienna, Austria. http:// www.R-project.org/.

Saavedra, S., Stouffer, D. B., Uzzi, B., & Bascompte, J. (2011). Strong contributors to network persistence are the most vulnerable to extinction. *Nature*, 478(7368), 233-235.

Vázquez, D. P., Lomascolo, S. B., Maldonado, M. B., Chacoff, N. P., Dorado, J., Stevani, E. L., & Vitale, N. L. (2012). The strength of plant-pollinator interactions. *Ecology*, 93(4), 719-725.

Vázquez, D. P., Poulin, R., Krasnov, B. R., & Shenbrot, G. I. (2005). Species Abundance and the Distribution of Specialisation in Host-Parasite Interaction Networks. *Journal of Animal Ecology*, 74(5), 946-955.

Vidal, M. M., Hasui, E., Pizo, M. A., Tamashiro, J. Y., Silva, W. R., & Guimaraes Jr., P. R. (2014). Frugivores at higher risk of extinction are the key elements of a mutualistic network. *Ecology*.

## CHAPTER FOUR

**How species abundance influences interaction strength in a bird-tree pollination network at Ngel Nyaki forest.**


## ABSTRACT

Most studies have used the frequency of interaction of one species on another as a measure of interaction strength (IS). This approach assumes that an interaction frequency between species is a good predictor of a species impact (i.e. flower visit frequency and pollen load transport). This is not neccessary the case in mutualistic interactions such as pollination, since most flower visits by some individuals or species result in variable effects that may be harmful to the host.

Here I considered two components of pollination: visitation and pollen transport. I then investigated how the overall impact of a species is influenced by a species' abundance. Finally, I identified the level of specialisation of each species. There was more specialisation in the PTN than in the FVN, which suggest that FVN often involved interactions that are antagonistic such as nectar robbing, insectivory and pollen theft. The strongest contributor to IS for FVN was not the same for the PTN, this indicates that the two measures of IS provide complementary information on species interactions. Abundance was a good determinant of IS in the (FVN) but not in the (PTN). My results emphasise the need for a combine approach for a holistic understanding and evaluation of crucial pollinators with regards to overall impact.


### 4.0: Introduction

In this study I tested the concept of interaction strength on two components of pollination; flower visitation frequency, and pollen transport efficiencies of sunbird species in a remote

Afromontane forest reserve. I investigated how the overall impact (i.e. flower visit frequency and pollen load transport) of a species derived from the two components of pollination is influenced by a species relative abundance. The concept of interaction strength (IS) was originally developed to illustrate how food webs are structured and to explain how biological systems are organised and sustained (Vázquez et al., 2012; Vázquez et al., 2005).

Most studies have used the frequency of interaction of one species on another as a measure of IS (Sahli & Conner, 2006; Stang et al., 2006; Vazquez et al., 2007; Vázquez et al., 2005). This assumes that an interaction frequency between species is a good predictor of species impacts. This is not necessarily the case; some flower visitors harm plants. Notable examples include nectar thieves, florivores, pollen wasters and visitors that dislodge pollen previously deposited on stigma: (Irwin et al., 2010; Morris et al., 2010).

I will distinguish two components of IS (see 4.2. for details):

**Visitation**

The visitation component of interaction strength is defined as the proportion of individuals of a pollinator species observed visiting a focal tree species, relative to all other visitors to the focal tree species. Therefore, using this definition, birds that visited a tree species less frequently than those species that visited more often, have a lower IS.

**Transport**

The transportation component of interaction strength is defined as the proportion of conspecific pollen (i.e. pollen from flowers of the same tree species) transported by a pollinator relative to pollen from the same tree species transported by other pollinators (Alarcón, 2010).

The pollen transport component of IS, reflects the reproductive fitness benefits of the interaction to the plants.

### 4.1: **The nature of interaction strengths**

In natural systems, most interactions are weak but a few are strong (Bascompte et al., 2006; Wootton, 1997). Most mutualistic interactions between plants and their pollinators are asymmetrical, i.e. contributions made by some partners outweigh the benefits they receive in return for their contributions (Bascompte et al., 2003; Bascompte et al., 2006; Vázquez & Aizen, 2004). This results in many strong interactions, many weak interactions and relatively few interactions of intermediate strength. This suggests a few strongly interacting species exert the most influence on ecological properties such as stability of the pollination network (Vazquez et al., 2007). However, it has become clear that weak links buffer networks against cascading failures and contribute to overall network stability (i.e. able to withstand perturbation) (Csermely, 2004; Csermely, 2009; Jason, 2013; Tylianakis, 2009).

### 4.1.1: How species abundance affects IS

Calculating IS from interaction frequencies can be misleading because estimates of interaction frequencies are often sampling artefacts such as insufficient sampling of rare interactions (Vazquez et al., 2009; Dorado et al., 2011). In plant-pollinator systems a common bias is that rare visitors to flowers such as birds have a low probability of being observed, and thus may appear to be specialists, when, in fact, they are generalists (e.g. Mayfield et al., 2001). This can result in underestimates of the influence of rare species.

## 4.2: Proxies for pollination efficiency

Despite the problems described above, visitation frequency is relatively simple to measure. As a result it is still one of the most often used proxies for pollination efficiency (Dupont et al., 2003; Olesen et al., 2008; Stang et al., 2006; Vázquez et al., 2012; Vazquez et al., 2007). Most discussions on the use of proxies for pollinator efficiency have favoured the incorporation of two or more proxies rather than relying on one (Alarcón, 2010; Popic et al., 2013; Vázquez et al., 2012).

Several other proxies for pollinator efficiency have been explored in the past, including; contact with reproductive structures (Gibson et al., 2011); measurement of visit duration (Kaiser-Bunbury et al., 2010); pollen removal (Popic et al., 2013); abundance/visitation rates (Stang et al., 2006). A common drawback of these proxies is that, in all methods, there is no assurance that pollen eventually lands on a receptive stigma. In addition, there is no absolute measure of success to account for seed-set (the ultimate yardstick for measuring reproductive fitness), (but see Geerts & Pauw, 2009a; Vazquez et al., 2012).

### 4.2.1: Indices of specialisation and the role of species abundance.

I have used the discrimination index d' to measure specialisation (Dormann, 2011; Dormann et al., 2009; Dormann et al., 2014). The discrimination index corrects for availability (abundance), making it the most suitable index for comparing specialisation within a network comprising rare and abundant species and across networks (Dormann, 2011). In addition d' is simpler than other comparable methods (E.g. degree or number of partners of a species, PSI-pollination service index, NSI-node specialisation index and Shannon's H), because it does not depend on a null model for cross-network comparison (Dormann, 2011).

## 4.3: Aim and Objectives

The main aim of this study is to determine the effect of species abundance on the relative contributions (interaction strength) of different sunbird species to the pollination of tree species using per-species pollen load transport and per-species flower visit frequency as predictors.

To answer this question I:

1. Estimate two components of interaction strength between plants and pollinators: visitation frequency and pollen transportation.
2. Identify level of specialisation (number of interaction partners) for plant and pollinator species.
3. Determine the level of variation in IS among species in each network

I hypothesised that:

i). If abundance has no effect on estimation of IS, then species with a high frequency of visitation will not differ in IS with species that visit less often.

## 4.4: Materials and Methods

STUDY SITE **(**refer to Chapter two for a detailed description**)**

The study was conducted at Ngel Nyaki Forest Reserve ($07^{o}$ 05'N $11^{o}$ 04'E) located at the eastern edge of the Mambilla Plateau in Taraba state Nigeria (Fig 1.3) at an elevation of approximately 1550 m a.s.l (Chapman & Chapman, 2001). Ngel Nyaki Forest Reserve is 46 $km^2$ in extent, of which *c*.7.5 $km^2$ comprises montane/submontane forest (Chapman &

Chapman 2001). The forest is surrounded by overgrazed grassland and savannah as well as associated riparian forests (Dowsett-Lemaire, 1989).

The fauna of Ngel Nyaki is part of the globally important Cameroon mountain range, as can be seen in the avifaunal composition, e.g. Cameroon sunbird *Cyanomitra oritis*, Bamenda apalis *Apalis bamendae*, Cameroon olive pigeon *Columba sjostedti*, Bannerman's weaver *Ploceus bannermani* etc. These species are typical of the Cameroon mountain region. Some of these species like *Ploceus bannermani* are threatened with extinction (Birdlife International, 2012) while others are range-restricted and endemic species of high elevation forests, unique to the Ngel Nyaki/Cameroon montane eco-region. (Fishpool & Evans, 2001; Manu et al., 2010). Apart from its status as an EBA (Endemic Bird Area), Ngel Nyaki Forest is also one of the most species rich of the 27 IBAs (Important Bird Areas) in Nigeria (Fishpool & Evans; Manu et al., 2010).

The high level of endemism makes the Ngel Nyaki forest a good habitat for this study, because understanding the level of cooperative interactions between these endemic trees and bird species might reveal some unique interactions typical of this forest and provide some useful insights to their conservation.

**Focal Observation and Mist-netting**

Refer to chapter three for details of flower visitation observation and bird trapping for pollen extraction. The flower visitation data was used to estimate the FVN interaction strength, while the pollen load data was used for PTN.

## 4.5: Data Analysis

### Question 1): Estimation of Interaction strength

Interaction strength was estimated for each of the two components of pollination (visitation and pollen transport). The visitation component of interaction strength is defined as the proportion of individuals of a pollinator species observed visiting a focal tree species, relative to all visitors to tree species. The transportation component of interaction strength is defined as the proportion of conspecific pollen (I.e. pollen from flowers of the same tree species) transported by a sunbird species relative to pollen from the same tree species transported by all sunbird species (Alarcón, 2010). Only species that were observed visiting flowers and also captured with pollen on their bodies were included in the analysis. Of the nine species captured in mist nets, only five species were common to both flower visitation and pollen transport networks.

To determine the interaction strength of animal visitors $P_{ij}$, I calculated the proportion of visits between 'j' and 'i', relative to i's total visits from all species (Dormann, 2011; Jordano, 1987). The derived values represent the dependence of each plant on each pollinator- hereinafter described as IS (interaction strength) see Equation 4.1 below.

$$\text{IS between plant i and animal j} = P_{ij} = a_{ij} / \sum_i a_{ij} = \text{IS}$$

Equation 4.1

Where:

$a_{ij}$ = frequency of interactions between species i and j; where i = plant, j = pollinator and P*ij* = Interaction strength.

To obtain the total interaction strength of a species $TS_j$ for a given network, I summed the result obtained above (i.e. visitor 'j's' strength on plant 'i') across all the plant species that visitor 'j' interacted with. This is given as the sum of dependencies or total strength. See equation 4.2 below: where: $TS_j$ = Total strength of a pollinator and P*ij* = Interaction strength.

$$TS_j = \sum_i P_{ij} \qquad \text{Equation 4.2}$$

High $TS_j$ indicates a high importance of a pollinator for the plants in the network.

The same approach was repeated for the pollen transport network. When comparing interaction strength and other species-level index values between visitation and pollen transport networks, I excluded species that were absent in either networks (Alarcón, 2010). For a measure of a species overall or net 'pollination' interaction strength (i.e. two components of pollination combined); I added the total interaction strengths for pollen transportation and flower visitation networks (i.e. $TS_j$ (FVN) + $TS_j$ (PTN)). See equation 4.3 below:

$$NS_j = \sum_i TS_j(FVN) + TS_j(PTN) \qquad \text{Equation 4.3}$$

Where $NS_j$ = Net strength or overall pollinator strength. FVN and PTN = the flower visitation and pollen transport network respectively.

**Question 3): Estimate plant and pollinator specialisation**

To determine the level of specialisation with respect to flower visitation frequency and pollen load estimation I used the "species level" function in bipartite package (R core team version 2.15.3 (2013) which calculates the discrimination index d' derived from the Kulback-Leibler distance (Dormann et al., 2014; Dormann et al., 2009). d' calculates how strongly a species

deviates from a random sampling of the interacting partners available. It ranges from 0 (no specialisation, implying that selection is totally random) to 1 (perfect specialisation).

The idea behind the derivation of d' is described in Blüthgen et al. (2006). d' calculates the Shannon-diversity for each column and re-arranges raw values (Blüthgen et al., 2006). It works based on the assumption that all partners are used relative to their availability. Following Blüthgen et al. (2006).

$$d_i = \sum_{j=1}^{c} S'_{ij} log_e(S'_{ij}/q_i)$$

$$d'_i = \frac{(d_i - d_{min})}{(d_{max} - d_{min})}$$ Equation 4.4

Where j = pollinator species i = plant species

d' = specialisation index,

$q_i$ = overall partner availability

$S'_{ij}$ = proportion of the number of interactions ($a_{ij}$) in relation to the respective row total (plant total).

My choice of d' is due to the fact that it is the only index where null models are not required, since it corrects for availability by its definition (Dormans 2011): that is, d' takes into consideration a species' relative abundance and calculates specialisation by standardising each species specialisation based on Shannon-Wiener in such a manner that species that are rare would not be automatically treated as specialist and abundant species would not be seen

as generalist by default. However, despite the fact that d' corrects for availability before the derivation of a species' specialisation value, a null model may still be required to statistically assess the significance of the specialization value, thus allowing for the positioning of the observed relative to a perfect generalist (Dorman, 2011; Bluthgen et al., 2006).

I used a null model following (Bluthgen et al. 2006), to determine whether specialisation level was higher than expected at random. Specialisation in interaction networks is twofold. Firstly, the community or network level specialisation $H_2$ (a measure based on bipartite representation of a two mode network of interactions such as plant – pollinator, where members of each group interact with members of the other group but not among themselves) (Bluthgen et al. 2006).

Secondly, the species level specialisation *d*' (the weighted form of the average number of links per species (L), is often interpreted as deviations of actual interaction frequencies from a null model which assumes that all partners are used in proportion to their availability. Both measures of specialisation range from 0 (most generalised) to 1.0 (most specialised) (Bluthgen et al. 2006).

Since the degree of specialisation of the entire network ($H_2$), equals the weighted sum of the specialisation of its elements (i.e. interacting species) or ($d_i$) (Bluthgen et al. 2006); I tested the significance of specialisation using a null model based on the network-level specialisation ($H_2$), because it is more amenable to the null model, (Dalsgaard et al. 2011).

$H_2$ was tested against a null model of random associations ($H_2$ran). 10,000 random permutations of the matrix was performed using *r x c* randomisation algorithm (Bluthgen et al. 2006), also see Patefield, (1981). In the null model, each species was assigned the same total number of interactions as in the observed matrix, but interactions were assigned at

random. The probability (*p*-value) that the observed network had a higher specialisation level than expected at random was calculated as the proportion of values obtained after 10,000 random permutations that were equal or larger than the specialisation value for the observed network (Bluthgen et al. 2006). See (http//rxc.sys-bio.net/) for more details of the methods and null model.

Paired sample t-test was used to test for a difference in specialisation between flower visitation and pollen transport interactions. The paired variables were dFVN and dPTN. The data met the assumptions of paired sample t-test (i.e. the mean difference of the paired variables was normally distributed.

**Question 4): Species level variations in IS for FVN and PTN**

Flower Visitation Network

I performed a univariate ANOVA to determine whether sunbird species differed in IS in the FVN. The residuals generated from the ANOVA model were tested to check for violations of the assumptions for parametric tests (i.e. normal distribution with histogram and Q-Q plot and equal variance with Levene's test). Both assumptions were met. In the model, FVN IS was the dependent variable while sunbird species was the fixed factor with five levels (variable sunbird, orange-tufted sunbird, northern-double-collared sunbird, green-headed sunbird and splendid sunbird).

Pollen Transport Network

To determine if sunbird species differed in IS in the PTN, I checked for any violations of the assumptions of parametric test. The residuals conformed to the linear fit expected under a

normal distribution. However, the assumption of homosdasticity (equal variances) was not met even after square-root transformation. I performed a Kruskal-Wallis H test, a non-parametric equivalent for ANOVA test. In this test, IS PTN was the test variable, while the grouping variable was sunbird species (with a range of 1-5). The asymptotic method was used to test for statistical significance.

To test for differences in Total IS (i.e. NS*j*) among sunbird species, I used a univariate ANOVA. I checked for any violations of assumptions of parametric tests. The residuals conformed to the linear fit expected under a normal distribution and the assumptions of equal variances were met. In the ANOVA model, PTN IS was the dependent variable, while sunbird species was the fixed factor with five levels (variable sunbird, orange-tufted sunbird, northern-double-collared sunbird, green-headed sunbird and splendid sunbird). I used sunbirds common to FVN and PTN (i.e. sunbird species that occurred in both networks, visited flowers and transported pollen), and tree species that interacted with these birds to calculate IS. Sunbird species that only visited flowers or only transported pollen (i.e. did not occur in both networks), were excluded in the analysis.

R statistical software, version 2.15.3, (R development core team, 2013) and IBM SPSS version 21.0 (IBM Corp, 2012) were used in all analyses.

**Test of hypothesis:**

i) Test whether IS depends on species relative abundance.

To test whether species relative abundance affects a species IS, I examined the relationship between FVN (IS) and total visits to tree species by each sunbird species. For the PTN, I examined the relationship between total number of birds captured with pollen of each tree species and the PTN (IS).

## 4.6: Results

There was a significant difference in IS among sunbird species for the flower visitation network ($F_{4, 16} = 3.19$, $p = 0.04$). There was no significant difference in IS among sunbird species in the pollen transport network ($\chi^2 = 8.26$, df = 4, $p = 0.08$). There was significant variation in NS*j* (net IS) (i.e. sum of FVN and PTN) of sunbird species ($F_{4, 16} = 3.30$, $p = 0.03$).

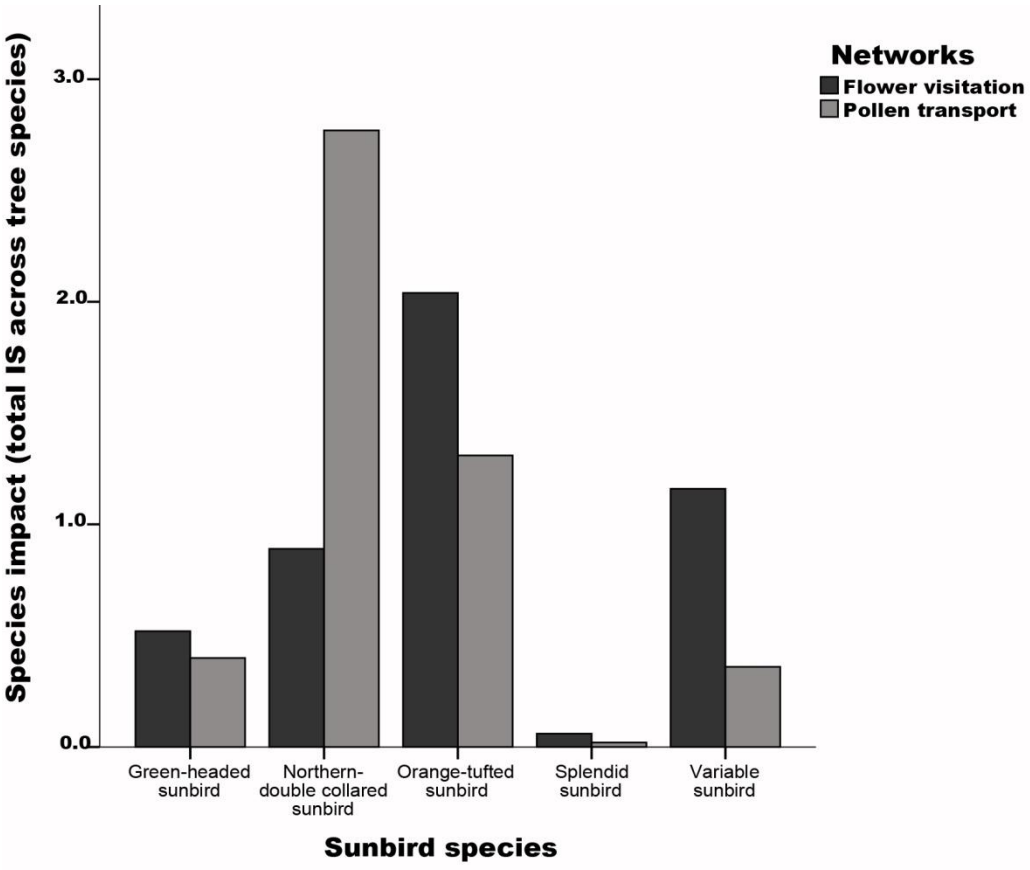



Figure 4.1: Variation in species total IS on tree species for the FVN and PTN. Bars represent total IS of sunbird species on five tree species that where common to both FVN and PTN. Black bars represent the FVN and grey bars the PTN.

**To test whether IS depends on species relative abundance**

We found a significant positive correlation between total visits to tree species and (IS) for FVN (Pearson coefficient = 0.75, N = 20, $p < 0.005$). Conversely, there was no significant correlation between number of individuals captured with pollen of each tree species and their respective (IS) for PTN (Pearson coefficient = 0.14, N = 15, $p = 0.63$).

**Specialisation for plant and pollinator species**

Null model permutations revealed a significant difference in species level specialization between the observed network and that generated at random after 10,000 permutations ($p = 0.001$) for the pollen transport network. However, there was no significant difference between the observed network and randomized networks (10,000 permutations) for the flower visitation network ($p = 0.99$).

Overall, the most specialised sunbird species in the flower visitation network was the splendid sunbird (d' = 0.36) while *Vitex doniana* (d' = 0.18) was the most specialised tree species. The pollen transport network had the green sunbird (d' = 0.42) and *Anthocleista vogelii* (d' = 0.37) as the most specialised for sunbird and tree species respectively. However, there was no significant difference in specialisation between the flower and pollen transport interactions, paired-sample t test (t = - 0.87, DF = 9, SD = 0.10, $p = 0.40$).

Table 4.1: Specialisation index d' of interacting species. FVN = Flower visitation network, PTN = Pollen transport network. Degree = number of links per species.

| Species | d? (FVN) | Degree (FVN) | d? (PTN) | Degree (PTN) |
|---|---|---|---|---|
| **Orange-tufted sunbird** | 0.13 | 11 | 0.14 | 7 |
| **Northern-double collared sunbird** | 0.09 | 12 | 0.14 | 9 |
| **Variable sunbird** | 0.08 | 12 | 0.15 | 7 |
| **Green-headed sunbird** | 0.2 | 7 | 0.22 | 3 |
| **Olive-bellied sunbird** | | | 0.16 | 1 |
| **Olive sunbird** | | | 0.21 | 1 |
| **Green sunbird** | | | 0.42 | 1 |
| **Collared sunbird** | 0.34 | 5 | | |
| **Splendid sunbird** | 0.36 | 2 | 0.2 | 2 |
| **Copper sunbird** | 0.34 | 2 | | |
| *Mistletoe* sp. | | | 0.01 | 2 |
| *Albizia gummifera* | 0.14 | 5 | 0.17 | 4 |
| *Nuxia congesta* | 0.08 | 4 | 0.06 | 7 |
| *Dombeya leadermanii* | 0.12 | 4 | 0.06 | 3 |
| *Anthercleista vogelii* | 0.11 | 4 | **0.37** | **1** |
| *Anthonotha noldeae* | **0.1** | **6** | 0.2 | 2 |
| *Syzygium guineense* | **0.05** | **3** | | |
| *Canthium* sp. | 0.09 | 4 | | |
| *Polyscias* sp. | 0.1 | 3 | | |
| *Dalbergia* sp. | 0.07 | 4 | | |
| *Harungana madagascariensis* | 0.17 | 2 | | |
| *Symphonia globulifera* | 0.05 | 5 | | |
| *Croton macrostachyus* | 0.09 | 5 | | |
| *Vitex doniana* | 0.18 | 1 | | |
| *Sterculia setigera* | 0.17 | 1 | | |
| *Lantana camara* | | | 0.16 | 3 |
| *Vine* sp. | | | **0.23** | **6** |
| Unknown pollen | | | 0.12 | 5 |

## 4.7: Discussion.

The results of this study suggest that my method of assessing strong and weak contributors on the basis of their combined contribution of flower visitation and pollen transport efficiencies was more realistic than using only visitation data. For instance, while some species displayed higher interaction strength in the FVN than in PTN, the strongest contributor to interaction strength for FVN, was not the strongest for the PTN. In addition, there was more specialisation in the PTN than in the FVN, because FVN often involve interactions with variable effects such as nectar robbing, insectivory and pollen theft. Therefore the two measures of IS provide complementary information on species interactions.

### Species relative abundance and IS

Based on the FVN, a quantitative network and good reflection of abundance, I found a significant correlation between species abundance and a species' IS ($p < 0.005$), implying that abundance determines a species' IS. Although other factors may also work in concert with abundance to determine strength, my result is consistent with the principle that abundant species have a higher probability of interactions and therefore have greater chances of affecting other species (Vazquez & Aizen, 2004).

### Abundance determines quantitative IS and not qualitative IS

With the FVN, I found a significant positive correlation between the total visits to tree species by sunbird species and their respective IS ($P < 0.005$), meanwhile, there was no significant correlation between total number of sunbirds captured with pollen and PTN interaction strength ($P = 0.63$). One possible reason for the lack of correlation between number of sunbird species captured and pollen transport IS, is because; pollen transport efficiency is invariant to the abundance of a species, as it reflects a measure of qualitative

contribution per bird. Thus, an efficient pollen transporter might surpass an abundant but less efficient species with regards to per-visit pollen transported. The total amount of pollen that a sunbird species transports would depend on abundance since the collective effort of many individuals would eventually surpass the efficient contributions of a few individuals in the long run.

**Abundance and quantitative IS are not related to qualitative IS**

My results show that sunbird species, e.g. green-headed sunbird, despite transporting the most pollen per bird (Chapter three), was among the least important in terms of overall PTN IS or total impact on host tree species due to their relatively low abundance (Appendix 4.5).

The low overall impact of green-headed sunbird suggest that the role of abundance as a proxy for assessing a species overall contribution would be more applicable to quantitative than qualitative components of pollination. This is because of the relationship between abundance and quantitative IS. This view is in line with similar studies where abundance was found to be a good proxy for studies of a quantitative nature, e.g. visitation frequency (Vasquez et al. 2005; Stang et al., 2006); and number of contact with reproductive parts (Gibson et al., 2011).

The observed difference in response to abundance between quantitative IS for FVN and qualitative IS for PTN could be due to the differences in data size (more visitation observation than pollen transport observation), which could pose a potential bias (Dormann et al., 2009). However, since pollen extraction took place during the same period with visitation observation, there was a good chance of recording the same interactions at the same frequency in both networks. It was easier to observe trees for floral visitors than it was to obtain pollen from sunbirds. Sunbirds are very restless and have a tendency to lose pollen while trapped in mist-nets, but, with insects there is more assurance of extracting a fair

amount of the original pollen. This is probably why past studies laid more emphasis on insects (Alarcón, 2010; Alarcón et al., 2008; Memmott, 1999; Popic et al., 2013; Stang et al., 2009; Vázquez et al., 2012). However, in most cases, emphasis was placed on insects rather than birds because of the absence of bird pollinators in some regions of the world. For example, in eastern North-America, there is at most one bird pollinator species-ruby-throated hummingbird (Austin, 1975).

My reliance on a simple sunbird-tree network in this study made it possible to investigate the efficiencies of species combining both the quantitative and qualitative component of pollination. Pollen load estimation though logistically challenging, is worth considering when measuring species efficiency, because it is closer to predicting host species fitness than visitation rates (Jacobs et al., 2010; Mayfield et al., 2001). King et al., 2013 argues that pollen assessment on the bodies of pollinators might be a poor representation of pollination potential and hence a poor indicator of a pollinator's status. However, other possible proxies such as, contact with reproductive structures (Memmott, 1999; Gibson et al., 2011), pollen removal (Alarcón, 2010), visit duration (Kaiser-Bunbury et al., 2010); share the same limitation - pollen loss. That is to say, none of these proxies provide information on the fate of the pollen carried by a pollinator. Even King et al., (2013)'s approach of single visit deposition (SVD) - a measure of the amount of pollen deposited on a stigma after a single visit to the anthers by a pollinator, projected as a better proxy for pollinator efficiency, falls short of meeting the ultimate goal; establishing fitness through seed-set. Despite the drawbacks of each approach, a combination of proxies (pollen load estimation and flower visit frequency), provides a more realistic approach than drawing conclusions from visitation frequency estimation alone.

**The relationship between FVN (IS) and PTN (IS)**

My assessment of the relative interaction strength of species revealed that the orange-tufted sunbird was the strongest contributor in FVN, while the northern-double collared sunbird was the strongest in PTN. Of the trees, *Anthonotha noldeae* contributed the most to FVN, while *Nuxia congesta* was the strongest contributor for PTN. A combined assessment of the relative interaction strength of species (i.e. a combination of proxies), revealed that northern-double collared sunbird and *Nuxia congesta* were the strongest contributors overall (i.e. combining IS for FVN and IS for PTN), from now on referred to as the "pollination network".

My results suggest that conclusions drawn from flower visitation frequencies as proxies for pollination are often misleading, because analyses of FVN may suggest that plants interact with more potential pollinators than they do in reality. Thus, a high IS for FVN as opposed to PTN by a given sunbird species could be an indication of the variable interactions such as nectar robbing, pollen theft and insect predation that often characterize the FVN. For instance, sunbirds foraging for insects may drive tree visitation patterns; thus, the presence of sunbird species on flowers is by no means an assurance of pollination. Our combination of FVN and PTN IS as proxies for pollination is therefore a more robust approach.

**Species specialisation.**

The index d' controls for a species' abundance and degree (number of links or partners) in its evaluation of a species' specialisation (Table 4.1). While specialisation is expected to decline as degree increases, we found that species with the same degree had different values of specialisation (d', see Table 4.1). In addition, one of the least specialised tree species, *Syzygium guineense* in the FVN, was not actually the most diverse with regards to interaction links or partners. Conversely, the most generalised tree species *Anthonotha noldeae* (with the most number of partners), was not the least specialised (Table 4.1). Similarly, *Albizia gummifera*, the second most connected species of the 14 tree species, was the third most

specialised surpassing several less connected species such as *Syzygium guineense* and *Polyscias fulva* (Table 4.1).

In addition to providing a degree-independent (invariant to a species abundance) measure of specialisation, our results for d' indicate that the two pollination networks are quite different (Table 4.1). From the null model to test the significance of specialization, results suggest that the pattern and degree of specialization displayed by species in the pollen transport network is driven by some biological or ecological process. On the contrary, species level specialization in the flower visitation network is largely driven by chance. Furthermore, the pollen transport network displayed more specialization at the network level (H2' = 0.22), and the species level than the flower visitation network (H2' = 0.15). This finding illustrates how inappropriate it is to evaluate a system based on a single proxy.

**Species dependencies and the implication for survival**

The fact that most sunbird species were relatively consistent in their IS for FVN and PTN (Appendix 4.1a & b), emphasises the importance of these tree species to sunbird species wellbeing.. However, the pattern of visitation (that is, high cumulative frequencies of visit from a wide range of sunbirds), observed on tree species such as *Nuxia congesta*, *Anthonotha noldeae, Albizia gummifera, Dalbergia* sp., and *Anthocleista vogelii*, could be an indication that these tree species are indeed dependent on these potential pollinators (sunbirds) for their reproductive success. However, at this stage the conclusions I make are guarded and restrained by the limitations typical of most studies associated with proxies. A key limitation of this study is my inability to monitor focal tree species until seed-set, which prevents me from measuring the relationship between flower visitation and seed production. In addition,

the difficulties associated with identifying conspecific pollen represent another source of error in my interaction strength calculations.

To the best of my knowledge, this is the first time a combination of proxies has been used to identify strong contributors, and the first time birds are exclusively considered in a network developed to address questions centred on network theory in an African montane forest. Elsewhere, previous studies (e.g. Alarcón, 2010; Pauw, 2007; Popic et al., 2013), used only insects as the experimental taxa. This study therefore provides insight on a taxonomic group (birds) and geographical region (Africa) that require more attention with regards to ecological network studies.

### 4.8: Conclusion

The aim of this chapter was to determine how the abundance of sunbird species influences their interaction strength in the bird-tree pollination network at Ngel Nyaki. My results show that interaction strength is dependent on the relative abundance of species. Although the efficiency of species measured through qualitative assessment such as pollen load on the bodies of sunbirds is invariant to abundance, differences in visitation rates implies that overall, abundance still affects interaction strength. Although some species were relatively stronger interactors in both networks, the strongest contributor for FVN was not the strongest for PTN. This finding demonstrates the importance of combining proxies when evaluating pollination efficiency. The strongest contributors for our combined "pollination network" are northern-double collared sunbird (pollinator) and *Nuxia congesta* (tree). The abundance and distribution of these two species at Ngel Nyaki would be a guarantee that specialist species by virtue of their spatio-temporal limitations would still be assured of reproductive fitness since strong contributors have a tendency to be encountered more often.

I have shown in this study that bird species that visit flowers more frequently do so for the obvious reward of floral resource (nectar, pollen and insects) and do not visit flowers at random, but have specific requirements that are met by a select few species among the many alternatives that abound in whatever ecological community they belong.

My results suggest that although logistically challenging, quantifying the amount of pollen transported on the bodies of bird species in addition to flower visitation frequency data will be a better and more realistic approach in determining strong and weak pollinators as well as beneficial and antagonistic interactions. This is reflected in the highly specialised PTN and in the complementary nature of each network. Ultimately, we should in future measure seed-set and even run field or nursery trials to test seed viability through seedling establishment. These additional steps, in concert with other measures taken or suggested in this study, will validate the conclusions drawn from studies of this nature and improve general understanding of pollination mutualism and pollination systems on a global scale.

# APPENDICES

Appendix 4.1a: Sunbird species flower visitation I.S on various tree species.

| S/N | Sunbird Species | Albizia | Anthocleista | Anthonotha | Dombeya | Nuxia | Total Strength |
|---|---|---|---|---|---|---|---|
| 1 | Orange-tufted | 0.68 | 0.32 | 0.17 | 0.28 | 0.59 | 2.04 |
| 2 | Northern-double collared | 0.05 | 0.12 | 0.38 | 0.11 | 0.23 | 0.89 |
| 3 | Variable | 0.11 | 0.22 | 0.28 | 0.4 | 0.15 | 1.16 |
| 4 | Green-headed | 0.12 | 0.32 | 0.07 | 0 | 0.01 | 0.52 |
| 5 | Splendid | 0 | 0 | 0.06 | 0 | 0 | 0.06 |

Appendix 4.1b: Sunbird species pollen transport I.S on focal tree species.

| S/N | Sunbird Species | Albizia | Anthocleista | Anthonotha | Dombeya | Nuxia | Total Strength |
|---|---|---|---|---|---|---|---|
| 1 | Orange-tufted | 0.62 | 0 | 0 | 0.44 | 0.25 | 1.31 |
| 2 | Northern-double collared | 0.12 | 1 | 0.88 | 0.44 | 0.33 | 2.77 |
| 3 | Variable | 0.04 | 0 | 0.11 | 0.11 | 0.1 | 0.36 |
| 4 | Green-headed | 0.22 | 0 | 0 | 0 | 0.18 | 0.4 |
| 5 | Splendid | 0 | 0 | 0 | 0 | 0.02 | 0.02 |

Appendix 4.2a: Tree species flower visitation IS on sunbird species

| S/N | Tree Species | OTSB | NDSB | VSBD | GHSB | SPSB | Total Strength |
|---|---|---|---|---|---|---|---|
| 1 | Albizia | 0.26 | 0.03 | 0.07 | 0.23 | 0 | 0.59 |
| 2 | Nuxia | 0.34 | 0.24 | 0.14 | 0.03 | 0 | 0.75 |
| 3 | Dombeya | 0 | 0 | 0 | 0 | 0 | 0 |
| 4 | Anthocleista | 0.09 | 0.06 | 0.1 | 0.44 | 0 | 0.69 |
| 5 | Anthonotha | 0.05 | 0.2 | 0.13 | 0.1 | 0.86 | 1.34 |

Appendix 4.2b: Tree species pollen transport IS on sunbird species

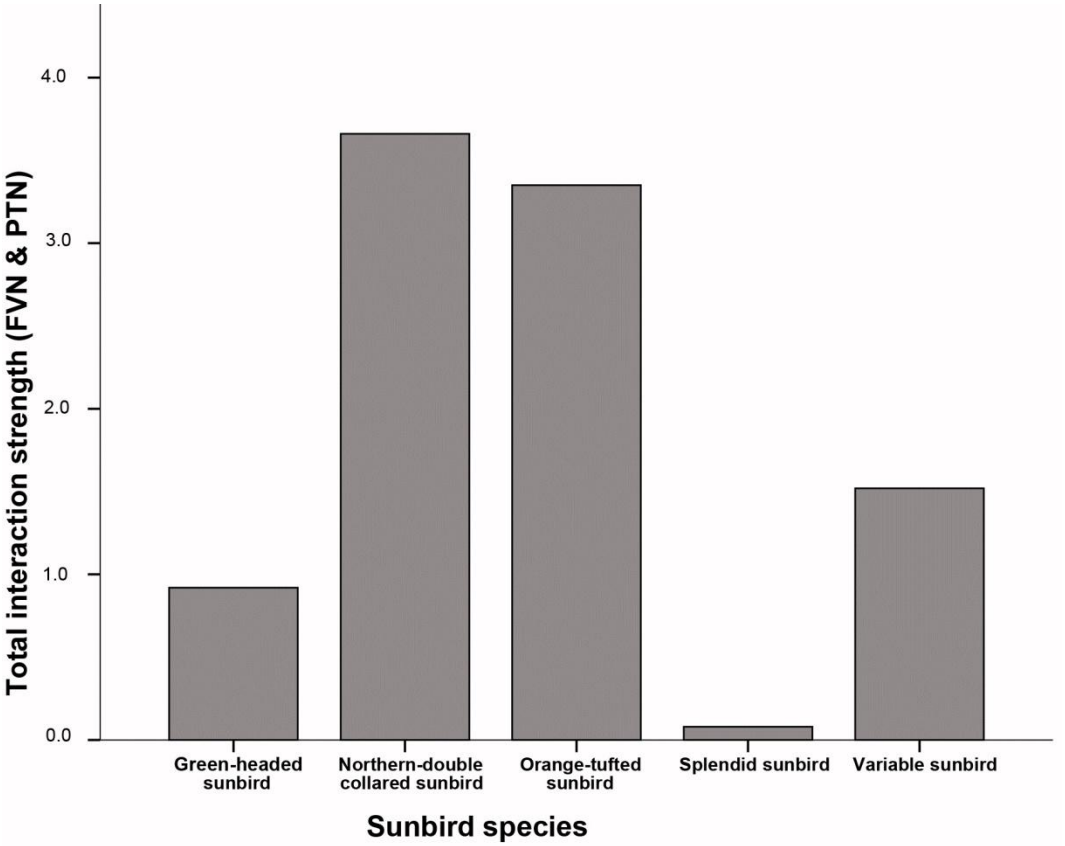
| S/N | Tree Species | OTSB | NDSB | VSBD | GHSB | SPSB | Total Strength |
|---|---|---|---|---|---|---|---|
| 1 | Albizia | 0.31 | 0.04 | 0.05 | 0.24 | 0 | 0.64 |
| 2 | Nuxia | 0.47 | 0.43 | 0.52 | 0.73 | 0.45 | 2.6 |
| 3 | Dombeya | 0.08 | 0.05 | 0.05 | 0 | 0 | 0.18 |
| 4 | Anthocleista | 0 | 0.17 | 0 | 0 | 0 | 0.17 |
| 5 | Anthonotha | 0 | 0.05 | 0.02 | 0 | 0 | 0.07 |

Appendix 4.3: Cumulative frequency and partner diversity of interacting species for FVN. Values represent number of flowers visited by several individuals of a species.

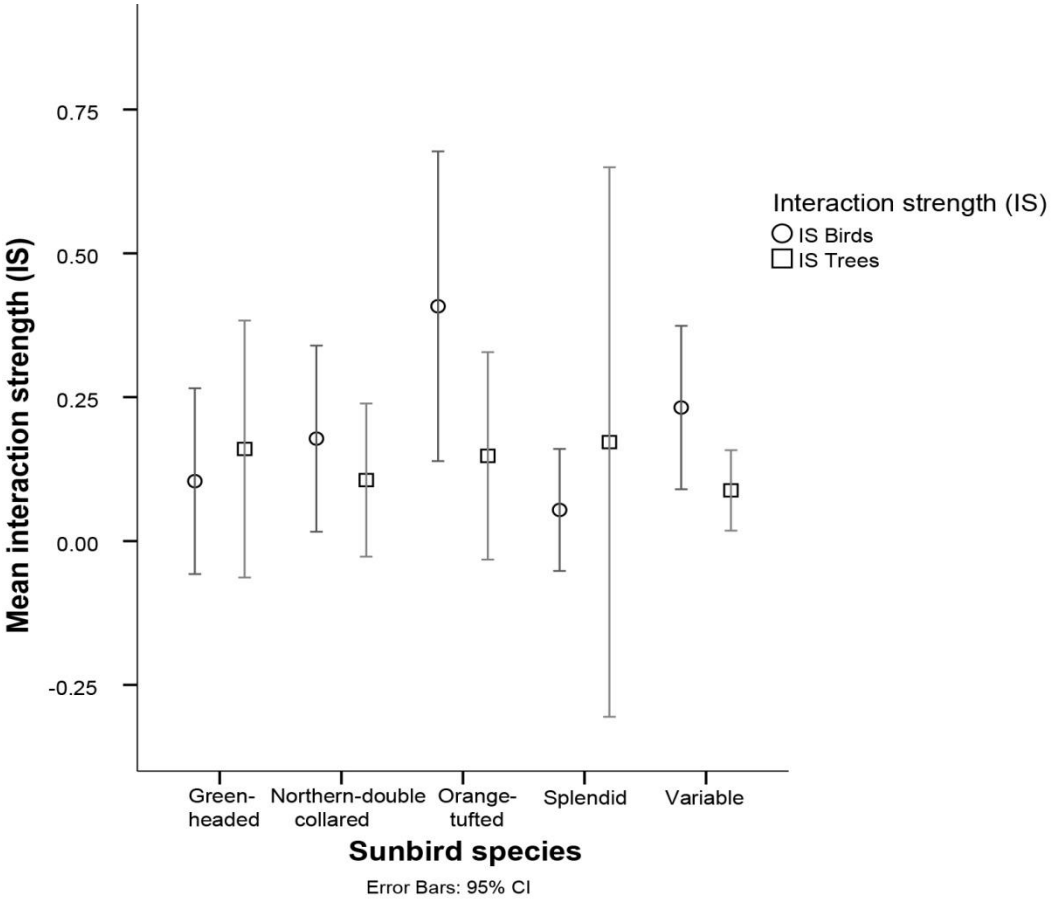
| S/N | SPECIES | OTSB | NDSB | VSBD | GHSB | CLSB | SPSB | COSB |
|---|---|---|---|---|---|---|---|---|
| 1 | Albizia gummifera | 2903 | 214 | 505 | 535 | 58 | 0 | 0 |
| 2 | Nuxia congesta | 3746 | 1469 | 957 | 74 | 0 | 0 | 0 |
| 3 | Syzygium guineense | 202 | 22 | 114 | 0 | 0 | 0 | 0 |
| 4 | Dombeya ledermannii | 10 | 4 | 14 | 0 | 7 | 0 | 0 |
| 5 | Canthium sp. | 5 | 25 | 12 | 0 | 4 | 0 | 0 |
| 6 | Polyscias fulva | 8 | 1 | 0 | 0 | 1 | 0 | 0 |
| 7 | Anthocleista vogelii | 1028 | 406 | 711 | 1019 | 0 | 0 | 0 |
| 8 | Dalbergia sp. | 1597 | 1465 | 2547 | 215 | 0 | 0 | 0 |
| 9 | Anthonotha noldeae | 562 | 1235 | 919 | 235 | 0 | 212 | 60 |
| 10 | Harungana madagascariensis | 0 | 24 | 113 | 0 | 0 | 0 | 0 |
| 11 | Symphonia globulifera | 681 | 1213 | 788 | 182 | 0 | 34 | 0 |
| 12 | Croton macrostachyus | 68 | 6 | 0 | 7 | 1 | 0 | 3 |
| 13 | Vitex doniana | 0 | 0 | 13 | 0 | 0 | 0 | 0 |
| 14 | Sterculia stigera | 0 | 0 | 10 | 0 | 0 | 0 | 0 |
| 15 | Newtonia buchananii | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 16 | Deibolia pinnata | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

Appendix 4.4: Quantity of pollen of various tree species removed from the body of captured sunbird species. Sunbird species are listed at the top row while tree species are on the second column.

| S/n | Species | OTSB | NDSB | VSBD | GHSB | SPSB | OBSB | OLSB | GRSB |
|---|---|---|---|---|---|---|---|---|---|
| 1 | Albizia gummifera | 31 | 6 | 2 | 11 | 0 | 0 | 0 | 0 |
| 2 | Nuxia congesta | 46 | 60 | 18 | 33 | 5 | 7 | 11 | 0 |
| 3 | Dombeya ledermannii | 8 | 8 | 2 | 0 | 0 | 0 | 0 | 0 |
| 4 | Anthocleista vogelii | 0 | 25 | 0 | 0 | 0 | 0 | 0 | 0 |
| 5 | Anthonotha noldeae | 0 | 8 | 1 | 0 | 0 | 0 | 0 | 0 |
| 6 | Unknown pollen | 2 | 12 | 1 | 1 | 0 | 0 | 6 | 0 |
| 7 | Lantana camara | 1 | 11 | 9 | 0 | 0 | 0 | 0 | 0 |
| 8 | Mistletoe sp. | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 9 | Red vine | 7 | 8 | 1 | 0 | 6 | 0 | 2 | 5 |



Appendix 4.5: Variation in total interaction strength of sunbird species. Bars represent sum of IS for FVN and PTN.




Appendix 4.6: Reciprocal IS for sunbird and tree species. Squares represent IS of trees and circles represent IS of birds.

## REFERENCES


Alarcón, R., Waser, N. M., & Ollerton, J. (2008). Year-to-year variation in the topology of a plant–pollinator interaction network. *Oikos*, 117(12), 1796-1807.

Alarcón, R. (2010). Congruence between visitation and pollen-transport networks in a California plant–pollinator community. *Oikos*, 119(1), 35-44.

Austin, D. F. (1975). Bird flowers in the eastern United States. *Florida Scientist*, 38, 1-12.

Bascompte, J., Jordano, P., Melián, C. J., & Olesen, J. M. (2003). The Nested Assembly of Plant-Animal Mutualistic Networks. *Proceedings of the National Academy of Sciences of the United States of America*, 100(16), 9383-9387.

Bascompte, J., Jordano, P., & Olesen, J. M. (2006). Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science*, 312(5772), 431-433.

BirdLife International. (2013). *State of the World's Birds*: Indicators for our changing world. Cambridge, UK, BirdLife International, Pg 9.

Blüthgen, N., Menzel, F., & Blüthgen, N. (2006). Measuring specialisation in species interaction networks. *BMC ecology*, 6(1), 9.

Castellanos, M. C., Wilson, P., Keller, S. J., Wolfe, A. D., & Thomson, J. D. (2006). Anther Evolution: Pollen Presentation Strategies When Pollinators Differ. *The American Naturalist*, 167(2), 288-296.

Chapman, J. D., & Chapman, H. M. (2001) *The Forests of Taraba and Adamawa States, Nigeria. An Ecological Account and Plant Species Checklist*. University of Canterbury, Christchurch, New Zealand.

Csermely, P. (2004). Strong links are important, but weak links stabilise them. *Trends in Biochemical Sciences*, 29(7), 331-334.

Csermely, P. (2009). *Weak links*: the universal key to the stability of networks and complex systems.

Dalsgaard, B. , Magård, E., Fjeldså, J., Martin González, A. M., Rahbek, C., Olesen, J. M., . . . Svenning, J. C. (2011). Specialization in plant-hummingbird networks is associated with species richness, contemporary precipitation and Quaternary climate-change velocity. *PloS one*, (6), e25891.

Dorado, J., Vázquez, D. P., Stevani, E. L., & Chacoff, N. P. (2011). Rareness and specialisation in plant-pollinator networks. *Ecology*, 92(1), 19-25.

Dormann, C. F. (2011). How to be a specialist? Quantifying specialisation in pollination networks. *Network Biology*, 1(1), 1-20.

Dormann, C. F., Fründ, J., Blüthgen, N., & Gruber, B. (2009). *Indices, Graphs and Null Models*: analysing bipartite ecological networks.

Dormann, C. F., Fruend, J., Gruber, B., Dormann, M. C. F., & LazyData, T. (2014). *Package 'bipartite'*

Dowsett-Lemaire, F. (1989). Physiography and vegetation of the highland forests of eastern Nigeria. A preliminary natural history survey of Mambilla Plateau and some lowland forests of eastern Nigeria. Ely, Tauraco Press (*Tauraca Research Report*, 1), 6-12.

Dupont, Y. L., Hansen, D. M., & Olesen, J. M. (2003). Structure of a plant–flower-visitor network in the high-altitude sub-alpine desert of Tenerife, Canary Islands. *Ecography*, 26(3), 301-310.

Elberling, H., & Olesen, J. M. (1999). The structure of a high latitude plant-flower visitor system: the dominance of flies. *Ecography*, 22(3), 314-323.

Fishpool, L. D., & Evans, M. I. (2001). *Important Bird Areas in Africa and Associated islands*: Priority sites for conservation. BirdLife International Cambridge, UK.

Geerts, S., & Pauw, A. (2009a). African sunbirds hover to pollinate an invasive hummingbird-pollinated plant. *Oikos*, 118(4), 573-579.

Geerts, S., & Pauw, A. (2009 b). Hyper-specialization for long-billed bird pollination in a guild of South African plants: the Malachite Sunbird pollination syndrome. *South African Journal of Botany*, 75(4), 699-706.

Gibson, M. R., Harris, C., Johson, S. D., Roux, J. J., Miller, J. T., Murphy, D. J., . . . George, N. (2011). Reproductive biology of Australian acacias: important mediator of invasiveness? *Diversity and Distributions*, 17(5), 911-933.

Harder, L. D., & Thomson, J. D. (1989). Evolutionary options for maximizing pollen dispersal of animal-pollinated plants. *American Naturalist*, 323-344.

Harder, L. D., & Wilson, W. G. (1994). Floral evolution and male reproductive success: optimal dispensing schedules for pollen dispersal by animal-pollinated plants. *Evolutionary Ecology*, 8(5), 542-559.

Irwin, R. E., Bronstein, J. L., Manson, J. S., & Richardson, L. (2010). Nectar robbing: ecological and evolutionary perspectives. *Annual Review of Ecology, Evolution, and Systematics*, 41, 271-292.

Jacobs, J. H., Clark, S. J., Denholm, I., Goulson, D., Staote, C., & Osborne, J. L. (2010). Pollinator effectiveness and fruit set in common ivy, Hedera helix (Araliaceae). *Arthropod-Plant Interactions*, 4(1), 19-28.

Janeček, Š., Patacova, E., Bartos, M., Padysakova, E., Spitzer, L., & Tropek, R. (2011). Hovering sunbirds in the Old World: occasional behaviour or evolutionary trend? *Oikos*, 120(2), 178-183.

Janecek, S., Pesata, M., Hrazsky, Z., Bartos, M., Brom, J., Reif, J., . . . Bystricka, D. (2007). Importance of big pollinators for the reproduction of two Hypericum species in Cameroon, West Africa. *African Journal of Ecology*, 45(4), 607-607.

Janeček, Š., Pesata, M., Mikes, V., Patacova, E., Altman, J., Kantorova, J., . . . Brom, J. (2012). Food selection by avian floral visitors: an important aspect of plant–flower visitor interactions in West Africa. *Biological Journal of the Linnean Society*, 107(2), 355-367.

Jason, M. T. (2013). The Global Plight of Pollinators. *Science*, 339(6127), 1532.

Jordano, P. (1987). Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. *American naturalist*: 657-677.

Kaiser-Bunbury, C. N., Traveset, A., & Hansen, D. M. (2010). Conservation and restoration of plant–animal mutualisms on oceanic islands. *Perspectives in Plant Ecology, Evolution and Systematics*, 12(2), 131-143.

King, C., Ballantyne, G., Willmer, P. G., & Freckleton, R. (2013). Why flower visitation is a poor proxy for pollination: measuring single-visit pollen deposition, with implications for pollination networks and conservation. *Methods in Ecology and Evolution*, 4(9), 811-818.

Manu, S., Imong, I. S., & Cresswell, W. (2010). Bird species richness and diversity at montane Important Bird Area (IBA) sites in south-eastern Nigeria. *Bird Conservation International*, 20(03), 231-239.

Mayfield, M. M., Waser, N. M., & Price, M. V. (2001). Exploring the 'most effective pollinator principle'with complex flowers: bumblebees and Ipomopsis aggregata. *Annals of Botany*, 88(4), 591-596.

Memmott, J. (1999). The structure of a plant-pollinator food web. *Ecology Letters*, 2(5), 276-280.

Morris, W. F., Vázquez, D. P., & Chacoff, N. P. (2010). Benefit and cost curves for typical pollination mutualisms. *Ecology*, 91(5), 1276-1285.

Olesen, J. M., Bascompte, J., Elberling, H., & Jordano, P. (2008). Temporal dynamics in a pollination network. *Ecology*, 89(6), 1573-1582.

Olesen, J. M., & Jordano, P. (2002). Geographic patterns in plant-pollinator mutualistic networks. *Ecology*, 83(9), 2416-2424.

Pauw, A. (2007). Collapse of a pollination web in small conservation areas. *Ecology*, 88(7), 1759-1769.

Popic, T. J., Wardle, G. M., & Davila, Y. C. (2013). Flower-visitor networks only partially predict the function of pollen transport by bees. *Austral Ecology*, 38(1), 76-86.

R Core Team. (2013). R: A language and Environment for Statistical Computing, R Foundation for statistical Computing, Vienna, Austria. http:// www.R-project.org/.

Saavedra, S., Stouffer, D. B., Uzzi, B., & Bascompte, J. (2011). Strong contributors to network persistence are the most vulnerable to extinction. *Nature*, 478(7368), 233-235.

Sahli, H. F., & Conner, J. K., (2006). Characterizing ecological generalisation in plant-pollination systems. *Oecologia*, 148(3), 365-372.

Stang, M., Klinkhamer, P. G., & Van Der Meijden, E. (2006). Size constraints and flower abundance determine the number of interactions in a plant–flower visitor web. *Oikos*, 112(1), 111-121.

Stang, M., Klinkhamer, P. G., Waser, N. M., Stang, I., & van der Meijden, E. (2009). Size-specific interaction patterns and size matching in a plant–pollinator interaction web. *Annals of Botany*, 103(9), 1459-1469.

Thomson, J. D. (2004). Perspectives on the evolution of sexual tactics in animal-pollinated plants: Pollen presentation theory and sex allocation theory. *Integrative and Comparative Biology*, 44(6), 652-652.

Thomson, J. D. (2006). Tactics for male reproductive success in plants: contrasting insights of sex allocation theory and pollen presentation theory. *Integrative and Comparative Biology*, 46(4), 390-397.

Tylianakis, J. M. (2009). Warming up food webs. *Science*, 323(5919), 1300-1301.

Vázquez, D. P., & Aizen, M. A. (2004). Asymmetric specialisation: a pervasive feature of plant-pollinator interactions. *Ecology*, 85(5), 1251-1257.

Vázquez, D. P., Blüthgen, N., Cagnolo, L., & Chacoff, N. P. (2009). Uniting pattern and process in plant-animal mutualistic networks: a review. Oxford University Press, England, pp. 1445-1457.

Vázquez, D. P., Lomascolo, S. B., Maldonado, M.B., Chacoff, N. P., Dorado, J., Stevani, E. L., & Vitale, N. L. (2012). The strength of plant-pollinator interactions. *Ecology*, 93(4),719-725.

Vazquez, D. P., Melian, C. J., Williams, N. M., Bluthgen, N., Krasnov, B. R., & Poulin, R. (2007). Species abundance and asymmetric interaction strength in ecological networks. *Oikos*, 116(7), 1120-1127.

Vázquez, D. P., Poulin, R., Krasnov, B. R., & Shenbrot, G. I. (2005). Species Abundance and the Distribution of Specialisation in Host-Parasite Interaction Networks. *Journal of Animal Ecology*, 74(5), 946-955.

Weston, K. A., Chapman, H. M., Kelly, D., & Moltchanova, E. V. (2012). Dependence on sunbird pollination for fruit set in three West African montane mistletoe species. *Journal of Tropical Ecology*, 28(2), 205-213.

Wilson, P., & Thomson, J. D. (1991). Heterogeneity among floral visitors leads to discordance between removal and deposition of pollen. *Ecology*, 1503-1507.

Wootton, J. T. (1997). Estimates and tests of per capita interaction strength: diet, abundance, and impact of intertidally foraging birds. *Ecological Monographs*, 67(1), 45-64.

# CHAPTER FIVE

## Differential contribution of sunbird species to the structure of a sunbird-tree flower visitation network predicts species survival and network stability.

## ABSTRACT

The survival of most species depends on networks of mutualistic partnerships with other species. As a result, understanding the stability of mutualistic networks is extremely important but so far has almost only been explored through theoretical and simulation studies, so that now empirical testing is necessary.

Theory suggests that network properties such as nestedness and connectance predict network stability. In particular, we expect the removal of species that contribute to either nestedness or connectance to harm network stability. Surprisingly, it has been shown that strong contributors to nestedness are the most prone to extinction.

Using an empirical sunbird - tree visitation network I tested whether a species contribution to nestedness was correlated with its extinction proneness. As predicted from network theory I found that in my empirical network strong contributors to nestedness were the rare species, which explains why they are most vulnerable to extinction. The implications of my findings are that in empirical networks nestedness will decrease overall through the loss of rare species but, from network theory this would not collapse the network as it is the common species, with the most links, which maintain network stability overall.

## 5.0: Introduction

Network structure (the pattern and arrangement of species in a given interaction) mediates the persistence of individual species within the network, and the persistence of the network as a whole (Bastolla et al., 2009; Csermely, 2009; Saavedra et al., 2011). While exact definitions of network persistence vary with context (e.g. Jordán & Scheuring, 2004; Alcántara & Rey, 2012; Stouffer & Bascompte, 2010 ) it generally refers to the *proportion of species that remain in a network at equilibrium* (Thébault & Fontaine, 2010).

It is very difficult to measure natural extinction processes in real time, therefore, extinction simulations have been used as tools to investigate network and species robustness to external perturbations (e.g. Bascompte & Stouffer, 2009; Bewick et al., 2013; Kaiser-Bunbury et al., 2010; Memmott et al., 2004; Saavedra et al., 2011; Thébault & Fontaine, 2010). The realism of these simulations is often limited. Recently Vidal et al. (2014) explored the possibility of using the status of a species on the IUCN conservation list as a way of determining a species' propensity to extinction. The IUCN status of species is determined based on several ecological criteria that are direct indicators of a species level of vulnerability or threat. Factors increasing the probability that a species will go extinct include a declining population, small population size, and small–range or area of occurrence (IUCN, 2012); also see Mace et al., (2008), for a detail review of IUCN risk assessment criteria. I used a modification of this approach in this study.

**Network architecture and stability**

In order to understand what makes mutualistic networks stable (i.e. the ability to withstand perturbation without collapse) they have been examined in terms of their topological organisation (Montoya et al., 2006; Thébault & Fontaine, 2010), the rationale being that the identification of key elements that structurally differentiate networks should point to the structures (configuration) and interactions that lead to network stability (Bascompte et al., 2003; Bastolla et al., 2009; May, 1972). Two key properties have been identified as the major predictors of network stability i) nestedness: defined as the tendency of ecological specialists to interact with a subset of species that interact with more generalist species and ii) connectance: defined as the number of observed links between species of plants and animals in a given network divided by the total number of potential links in the network (Allesina & Tang, 2012; Olesen et al., 2008). Tylianakis et al. (2010) are of the view that nestedness and connectance can be easily incorporated into conservation monitoring (Tylianakis et al., 2010). Nestedness is believed to promote species coexistence by reducing competition among interacting species (Bascompte et al., 2003; Saavedra et al., 2011), while increasing connectance stabilises a network (i.e. resistance to perturbation and extinction). Connectance is believed to be the key determinant of species and network persistence (James et al., 2012). Recent studies suggest that the removal of strong contributors to nestedness and connectance negatively affects network stability. There is still debate on whether nestedness or connectance best predicts network stability (i.e. being able to withstand perturbation) (see James et al., 2012; James et al., 2013; Saavedra & Stouffer, 2013).

I address two key issues: i) Use an empirical sunbird-tree visitation network to determine which metric (nestedness or connectance) best predicts network stability. ii). Test current

theoretical views on the fate of strong contributors to network stability (e.g. Saavedra et al., 2011). Other goals include:

1. Determine which sunbird species contribute the most to nestedness.
2. Determine the relationship between species contribution to nestedness and their connectance.

I hypothesised that: if nestedness depends on species degree or abundance, then rare species would contribute less to nestedness and would also be less connected than abundant species. I therefore expect to see a positive correlation between contribution to nestedness and connectance.

## 5.1: MATERIAL AND METHODS

STUDY SITE

The study was conducted at Ngel Nyaki Forest Reserve ($07^{o}$ 05' N $11^{o}$ 04' E) located at the eastern edge of the Mambilla Plateau in Taraba state Nigeria at an elevation of approximately 1550 m a.s.l (Chapman & Chapman, 2001). Ngel Nyaki Forest Reserve is 46 $km^2$ in extent, of which *c*.7.5 $km^2$ comprises montane/submontane forest (Chapman & Chapman 2001). The forest is surrounded by overgrazed grassland and savannah as well as associated riparian forests (Dowsett-Lemaire, 1989).

### Flower Visitation

In order to develop a sunbird/tree flower visitation network I observed a total of five individual trees for each of 14 tree species (Appendix 5.7) during times of the day when sunbirds are particularly active (6:30 am -12:30 pm, and 3:30 -5:30 pm). These observations were restricted to periods of peak flowering between 2011 and 2014 (Nigerian Montane Forest Project (NMFP) phenology data). Tree species were chosen based on flower availability. Observation periods were varied in order to address the disparity in flowering

phenology (i.e. irregular flowering cycles of individuals of a given species) and season. The aim was to collect data from as many flowering trees in the forest as was logistically feasible. To account for variation in spatial abundance and distribution of sunbird species, I selected focal trees from different parts of the forest. Trees were at least 100 metres apart from each other. Each individual tree was monitored for a period of 20 minutes during each observation session (i.e. morning or evening), amounting to 40 observation minutes per day. A total of 120 minutes (2 observation hours) was spent on each individual of all tree species. I alternated the order of observation to account for any possible biases that may arise from time of day.

We positioned ourselves approximately 25 metres away from a focal tree to avert possible distraction of the foraging activities of sunbird species. Each time birds were seen settling on tree, I recorded the number and identity of individuals, time of detection or arrival, number of flowers contacted and the time of departure. I summed the total number of individuals of each sunbird species that contacted flowers of various tree species to have the overall frequency of visitation by species. This data was used to develop the flower visitation network.

**Species diversity/abundance assessments**

A line transect census technique was used to estimate diversity and abundance of sunbirds found within the study site. Line transect sampling (Bibby et al., 2001) was carried out between 6:30 am -9:30 am) and between (3:30 -5:30 pm) each day. The survey took place between November, 2012 to February, 2013 and between November 2013 and February 2014. A total of 19 transects ranging between 336 m to 1,737 m in length and covering a total distance of 16.7 kilometres was surveyed. Transects were selected in order to include a representative sample of all habitat types in Ngel Nyaki reserve. I reasoned that by doing this I would also include a representative dataset of the diversity, abundance and distribution of

sunbird species in Ngel Nyaki reserve. Thirteen transects were located along the edges of the core forest on the eastern side of the reserve, while the other six were scattered within riparian fragments (Figure 2.2, chapter 2). Each transect was surveyed twice each season (November, 2012 - February, 2013, and November, 2013-February, 2014), making a total of four sessions per transect (morning and evening).

During each observation session, my field assistant and I walked slowly along each transect, recording birds seen to at least 50 m on either side of the transects. A pair of Nikon 9 x 40 binoculars was used to confirm the identity of birds located by eye. Only birds visually identified were included in the census data as it was difficult to estimate the actual number of individuals based on calls alone. I recorded the identity, number of individuals seen and time of sighting.

Information from my transect survey was used to categorize species on the basis of their population densities into abundant and rare species. Rarity was used as a proxy for extinction proneness (Vidal et al., 2014). In my classification, rare species by virtue of their low population size were considered to be more vulnerable to extinction than abundant species.

My simplified classification is based on three out of five criteria used to categorise species in the IUCN Red Data List (IUCN, 2012) see also Mace et al., (2008), for a detail review of IUCN risk assessment criteria. Although my categorisation was based on rarity alone, I reason that rare species would have at least one of the following attributes: i) small range area, ii) small population size and iii) very small population size. These attributes are three of five IUCN criteria for determining species that are at risk of extinction.

I defined an arbitrary threshold of abundance based on transect survey data. Species with number of individuals >100 were considered abundant, while those with number of

individuals < 100 were considered rare. This seemed reasonable as our data showed a big gap between rare (maximum number = 97) and abundant (minimum number = 356) (Appendix 5.2).

## 5.2: DATA ANALYSIS

**Network structure analysis:**

First, I combined the observed flower visits (cumulative visits by individuals of each species) to create a single pollinator by plant (S x T) matrix, or visitation network, in which the cell values represents the number of occasions individual sunbird visitors from species *S* were observed foraging on flowers of tree species *T* (Alarcon et al. 2008).

To calculate the nestedness of the sunbird-tree visitation network I used the bipartite package and the metric NODF (nestedness based on overlap and decreasing fill) (Almeida-Neto et al., 2008) in R statistical software version 2.15.3 (R development core team, 2013). With the "visweb" function, I generated a bipartite matrix to visualise the frequency and pattern of interactions in the network. Other network-level parameters such as connectance and number of links per species were determined using the "networklevel" function.

**The determination of which species of sunbird contributed the most to nestedness.**

Following the methods of Saavedra et al. (2011), I calculated the nestedness of the whole matrix, ($N_{tot}$) and then subtracted a second measure of nestedness ($N_i$*), calculated after randomising the contributions of each species i to the overall network nestedness ($N_{tot}$)

To compute the contribution of one animal species to the nestedness of the entire matrix I calculated the difference in the nested nodf scores between the observed matrix, and the

average nestedness score of 1000 matrices where the entries associated with the animal of interest had been randomised. For example, for bird species 1 (orange-tufted sunbird, figure 5.3) I made a copy of the original matrix. In this matrix bird species 1 can potentially pollinate *n* plant species. I extracted the scores for each of these *n* entries and re-assigned each score to a plant species at random. So that bird species 1 pollinates the same number of plant species, but the identity of the plants it pollinated has been randomised. I then determined the difference between the nestednodf score of the original, unrandomised matrix and the new randomised matrix. To create a null distribution for bird species 1, I repeated this procedure 1000 times. I then performed an equivalent calculation for the other bird species.

Nestedness contribution is the difference in the value of the original nestedness ($N_{tot}$), with that obtained ($N_i$*), when each species had its interactions randomised. These values ($N_i$*) were derived from a mean nestedness score after 1000 randomisation for each species. For details of the model equation, (see Appendix 5.1).

**Determine which species have the highest connectance**.

With the "specieslevel" function in bipartite package, I determined species connectance (Dormann et al., 2009). Values correspond to the realised interactions (degree or number of interaction partners) of a given species divided by the total number of possible mutualistic interactions (i.e. total number of prospective partners). The equation for network connectance is given as:

$$C = \frac{L}{IJ}$$ Equation 5.1

Where C = connectance, L = number of realised links in a network, and I = number of tree species, and J = number of sunbird species.

Individual species connectance was calculated separately for each group (Dorman et al., 2009), sunbird species connectance was calculated as:

$$C = \frac{A_j}{I}$$ Equation 5.2

Where: $A_j$ = total number of interactions of species j (Sunbirds) and I = number of tree species.

**Determine whether species that contribute the most to nestedness are the least likely to survive perturbations.**

I used an independent sample t test to test for a difference between the contribution to nestedness of rare species (species with less than 100 individuals) versus abundant species (species with greater than 100 individuals),

**Investigate the relationship between nestedness and connectance**

A linear regression was used to investigate the relationship between species contribution to nestedness and connectance. I also explored the relationship between rarity and connectance, using a linear regression and correlation analysis. I tested the hypothesis that if nestedness depends on species degree or abundance, then rare species would contribute less to nestedness and would also be less connected than abundant species. I therefore expect to see a positive correlation between contribution to nestedness and connectance.

## 5.3: Results

### Nestedness

The strongest and weakest contributors to nestedness were the copper sunbird *C. cupreus* and the northern-double collared sunbird *C. reichenowi* respectively. Surprisingly, these were the least (Copper sunbird) and most (northern-double collared sunbird) connected species in the network (Appendix 5.4).

There was no significant difference in nestedness contribution between rare and abundant species, (mean: 0.031 ± S.E 0.0005) for rare species and (mean: 0.004 ± S.E 0.01) for abundant species ($t(5) = -1.67$, $p = 0.15$) (Appendix 5.4). There was also a negative non-significant correlation between species contribution to nestedness and connectance

(coefficient = - 0.584, N = 7, p = 0.16). (Appendix 5.5). Overall, network nestedness (NODF value) was 73.23 (Appendix 5.3).

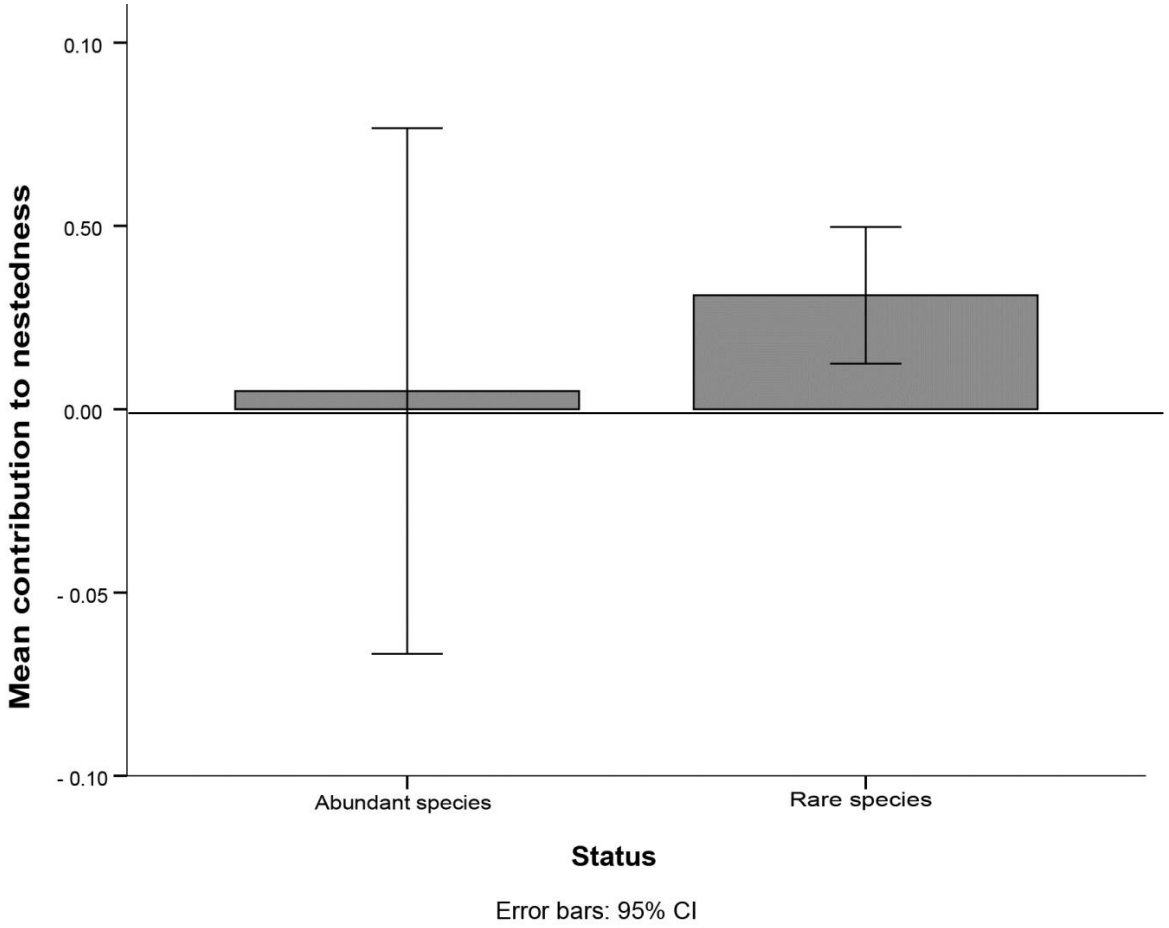



Figure 5.1: Mean contributions to nestednesss for abundant and rare sunbird species

## Connectance

The more abundant a species is in the network the more connected they are (i.e. had a higher connectance). The two most connected sunbird species were the variable sunbird *Cinnyris venustrus* and northern-double collared sunbird, both of which had a connectance value of 0.87, meaning that they each interacted with 87% of available tree species in the network.

The least connected sunbird species were copper sunbird and the splendid sunbird *C. coccinigastrus*, each of which had a connectance value of 0.14.

Overall network connectance was 0.52 (Appendix 5.3). I found a significant difference in mean connectance between rare (0.28 ± S.E 0.08) and abundant species (0.83 ± S.E 0.02), ($t(5) = 5.18$, $p < 0.005$).

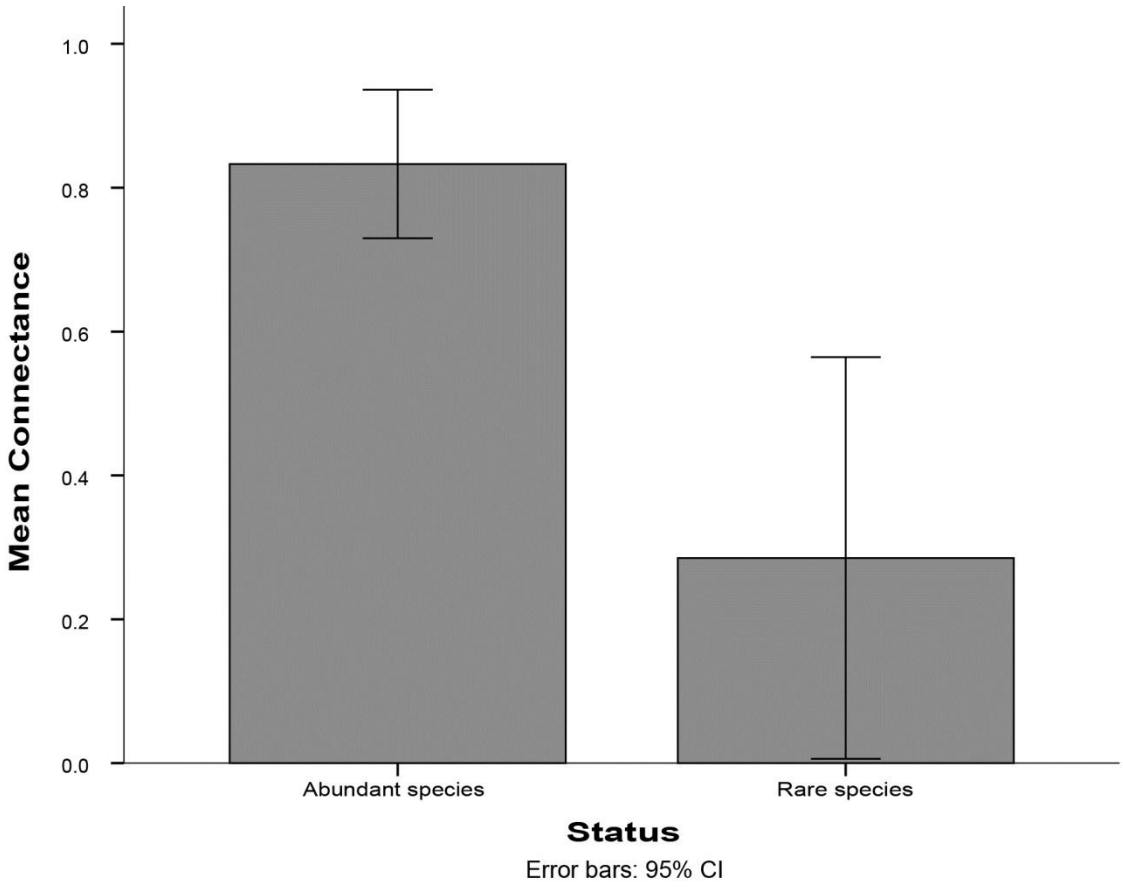



Figure 5.2: Mean connectance for abundant and rare species of sunbirds.

There was a significant positive correlation between a species abundance and its level of connectance (Pearson coefficient = 0.92, N = 7, $p < 0.005$). Conversely, I found a significant

negative correlation between a species rarity and its level of connectance (Pearson coefficient = - 0.92, N = 7, $p < 0.005$).

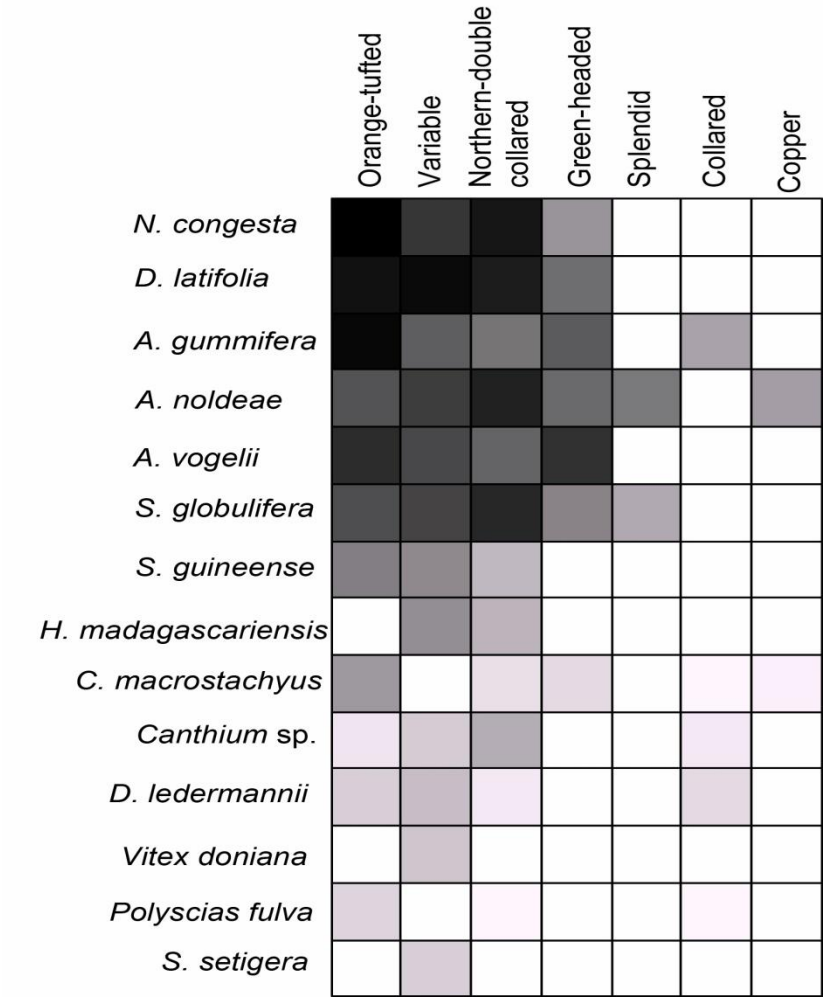



Figure 5.3: The matric structure of the flower visitation network showing the various interactions between sunbird and tree species at Ngel Nyaki forest. (the shaded boxes indicate an interaction between tree species and sunbird species. The depth of the shaded boxes represents the frequency of interaction. White boxes (empty boxes) = no interaction.

## 5.4: Discussion

One of the goals of this research was to use a simple sunbird- tree pollination network to explore how the key network properties of individual species in the network i) *nestedness* and ii) *connectance* affected species persistence and network stability. These particular

network properties were chosen because they are useful properties (Atmar & Patterson, 1993; Saavedra & Stouffer, 2013) and are relatively easily incorporated into conservation monitoring (Tylianakis et al., 2010). I tested current ideas on the implication of differential contribution to nestedness and connectance by individual species and the consequences for species survival and network persistence.

Previously, Saavedra et al., (2011) had found that the loss of species that contribute more to nestedness was more detrimental to network persistence than the removal of species that contribute less. Based on this background, nestedness contribution therefore represents a vital indicator of the level to which a species' interaction in a network affects the survival or persistence (positively or negatively) of other interacting species in the network (Saavedra et al., 2011).

**Fate of strong contributors to nestedness and network persistence**

My results provide a way to explore the relationship between nestedness, connectance and the natural histories of the focal species. In my network strong contributors to nestedness tended to be rare species with fewer partners and lower connectance. These trends were however non-significant. I used rarity as a surrogate to extinction proneness (See Vidal et al. 2014) and based on this rationale I am able to explain why species that contribute more to nestedness are thought to be the most prone to extinction. This is based on the premise that rare species have fewer partners (low connectance), and have a higher propensity to be affected by the loss of a partner. In other words, rare species have a high probability of secondary extinction: extinction due to the loss of a partner. Likewise, using connectance as a surrogate for a species survival as it directly equates to rarity/or abundance, we can easily

relate our results to Saavedra's conclusion on the negative correlation between species contribution to nestedness and survival.

My findings support a conclusion of previous studies, that a species' contribution to nestedness had a negative correlation with a species survival probability (Saavedra et al., 2011).

Contribution to nestedness was negatively correlated to connectance. Based on this result, I can say that the more a species contribute to nestedness, the lesser its chances of survival (Saavedra et al., 2011; Vidal et al. 2014). Conversely, my results also suggest that the higher the connectance of a species, the greater its chances of survival and the lower its connectance, the lower its chances of survival (James et al., 2012). Here, I focused on contribution to nestedness and connectance; whereas, previous studies have not. Based on this approach, I found that the term strong contributor to network structure is context dependent. My results indicate that strong contributors to nestedness were not strong contributors to connectance. These contextual differences should encourage us to be explicit on what we measure and to be careful with conclusions that presume a species identified as a weak contributor based on one metric (for e.g. nestedness), is generally less-crucial or weak across all metrics (Berlow et al., 2004), see also (Berlow, 1999; McCann, 2000).

My results highlight the importance of each species (rare or abundant, strong or weak) in shaping and sustaining the structure of a network, a trend that has been reported previously (McCann et al., 1998; Csermely, 2009; Tylianakis, 2009). Ironically, it does appear from the results of this study that rare species (weak links) with fewer partners are important in shaping the structure of the network through nestedness and as such could be major determinants of the survival of networks and species therein. This result is in accordance with current views suggesting that weak links act as buffers against perturbations and have the

capacity to stabilise networks (McCann et al., 1998, Tylianakis et al., 2007; Tylianakis, 2009).

Although it has been suggested that networks that are most resilient and, most able to survive external perturbations comprise many weak and a few strong interactions (McCann et al., 1998, Tylianakis, 2009); it does not rule out the importance of strong links, because the presence of strong links in a network is still a key requirement for stability and persistence. These views and the results of this study clearly support the idea that mutualistic networks are composed of many weak and few strong links and also often show nested patterns (Bascompte et al., 2003) in order to enhance and optimise network's intrinsic stability (Csermely, 2004; Tylianakis, 2009).

**Nestedness and connectance: why they are important**

Although my findings explains why strong contributors to nestedness are most vulnerable to extinction based on species abundance and/or rarity (Vidal et al. 2014), we are yet to unravel why rare species tend to contribute more to nestedness than abundant species. The implication of a species connectance on network stability and the effect on network/ species survival is much easier to comprehend than nestedness, and is favoured based on Occam's razor (the principle that, faced with two contentious explanations for some phenomenon, the simplest explanation should be chosen unless there are convincing reasons not to).

Connectance reflects species' rarity, and clearly explains a species' survival probability, contribution to nestedness did not in this study, and this is consistent with conclusions drawn from simulation studies that are of the view that contribution to nestedness is a poor predictor of network and species stability (e.g. James et al., 2012). Apart from the poor predictive power of nestedness, which is often improved with application of null models, in most cases translating the results obtained from a purely analytical framework into ecologically realistic

context is very daunting. This is probably because the ecological significance of a nested pattern in most empirical networks is still a progressing and highly contentious subject (James et al., 2012). In mutualistic networks, a high level of nestedness is believed to act as a buffer against secondary extinction (Tylianakis et al., 2010), and this is the reason why most studies suggest that nestedness has the capacity to ensure the stability/persistence of networks**.**

A highly nested network acts as a shield against temporal fluctuations in abundance of specialist pollinators (Tylianakis et al., 2010; Thebault & Fontaine, 2010). This could increase the survival probability of pollinators. It is crucial to identify factors likely to result in a highly nested network.

Staniczenko et al., (2013) suggest that, in a nested quantitative network, a generalist-generalist pair will contribute the most to nestedness or network stability, followed by a generalist-specialist, with the weakest being a specialist-specialist pair. Contrary to the views of Staniczenko et al. (2013), I observed from my simple sunbird – tree network that contribution to nestedness does not follow such a rigid and organised step-wise pattern (see figure 5.3), but some irregular and unique pair-wise configuration that de-emphasises species abundance. Thus a specialist – generalist combination can yield a higher nestedness than a generalist - generalist combination. However, I agree with Staniczenko et al., (2013) that a specialist – specialist combination will contribute the least to nestedness as well as link strength.

The proportion of weak to strong contributors (I.e. number of weak versus strong contributors) observed in this study, follows a trend which corresponds with results of other studies (e.g. Csermely, 2009) suggesting a higher proportion of weak contributors to strong ones in most ecological networks. Based on the observation that nestedness promotes biodiversity (Bascompte et al., 2006; Bascompte & Jordano, 2007; Bastolla et al., 2009). The

high level of nestedness I observe suggest that sunbird tree pollination network at Ngel Nyaki should be resilient and in fact robust to perturbations.

Rare species tend to contribute more to nestedness and this could be of interest to conservation biologists. However, in terms of interpreting the dilemma of strong contributors to network structure in a biologically realistic context, connectance is a better metric than nestedness. I recommend the incorporation of both properties into network models designed to address conservation issues as this would ensure that rare and abundant species are considered during conservation planning.

### 5.5: Conclusion

My findings emphasise the importance of weak links (rare species), in this case strong contributors to nestedness, and strong links (abundant or highly connected species). In the light of the above, copper sunbird and northern-double collared sunbird are the most crucial species in the sunbird-tree interaction network at Ngel Nyaki as they contextually represent the strongest contributors to network structure.

### Limitations

First, my network and data set was quite small and accounted for the lack of statistical significance observed between rare and abundant species with regards to nestedness, but see McQuaid & Britton, (2013). Future work should consider testing these findings with a larger data set to ensure a statistically robust conclusion.

Secondly, my visitation network is only a snap-shot of the real interaction network (Lawton, 1990), and only capture the structural pattern of the network for the period under

consideration. This is obvious because, most sunbird species are seasonal migrants, and flowering phenology is highly seasonal. At best what I have generated is a *motif* (sub-set) of the real visitation network; a complete network can only be feasible only after a year-long assessment to capture all interactions.

Finally, the fact that my assessment was based on a quantitative approach using rarity as a key factor, does not in any way preclude other qualitative factors (Mcquaid & Britton, 2013). Future research therefore should focus on investigating how these patterns (nestedness and connectance) interact with other determinants of network structure such as dietary preferences, phenology, and trait-matching. This approach would provide insights into the forces mediating network structure and how these forces affect the survival/stability of species and networks.

## APPENDICES.

Appendix 5.1: Detail of the model equation used to calculate sunbird species contribution to nestedness.

```
rm(list=ls())

flowW<-read.table("/My_documents/work/Nigerianetwork/birds
2014.csv",header=T,row.names=1,sep=",")
originalNodf<- nestednodf(flowW)$statistic[3]
nRandom<-1000

NstarAnimal<-matrix (NA, dim(flowW)[2],nRandom)

For (animal in 1:dim(flowW)[2]){
        For (i in 1:nRandom){
                flowW_c<-flowW
                flowW_c[,animal]<-
flowW_c[sample(dim(flowW_c)[1],replace=F),animal]
                modNodf<-nestednodf(flowW_c)$statistic[3]
                NstarAnimal[animal,i]<-modNodf
        }
}

meanNstarA<-apply(NstarAnimal,1, mean)
sdNstarA<-apply(NstarAnimal,1, sd)

networkContCorrected<-(originalNodf-meanNstarA)/sdNstarA
names(networkContCorrected)<-names(flowW)

rAb<-c("A","A","A","R","R","R","R")
t.test(networkContCorrected~ rAb)
```

Appendix 5.2: Risk categorisation and extinction proneness. Species in red where not part of the flower visitation network and were excluded in the analysis.

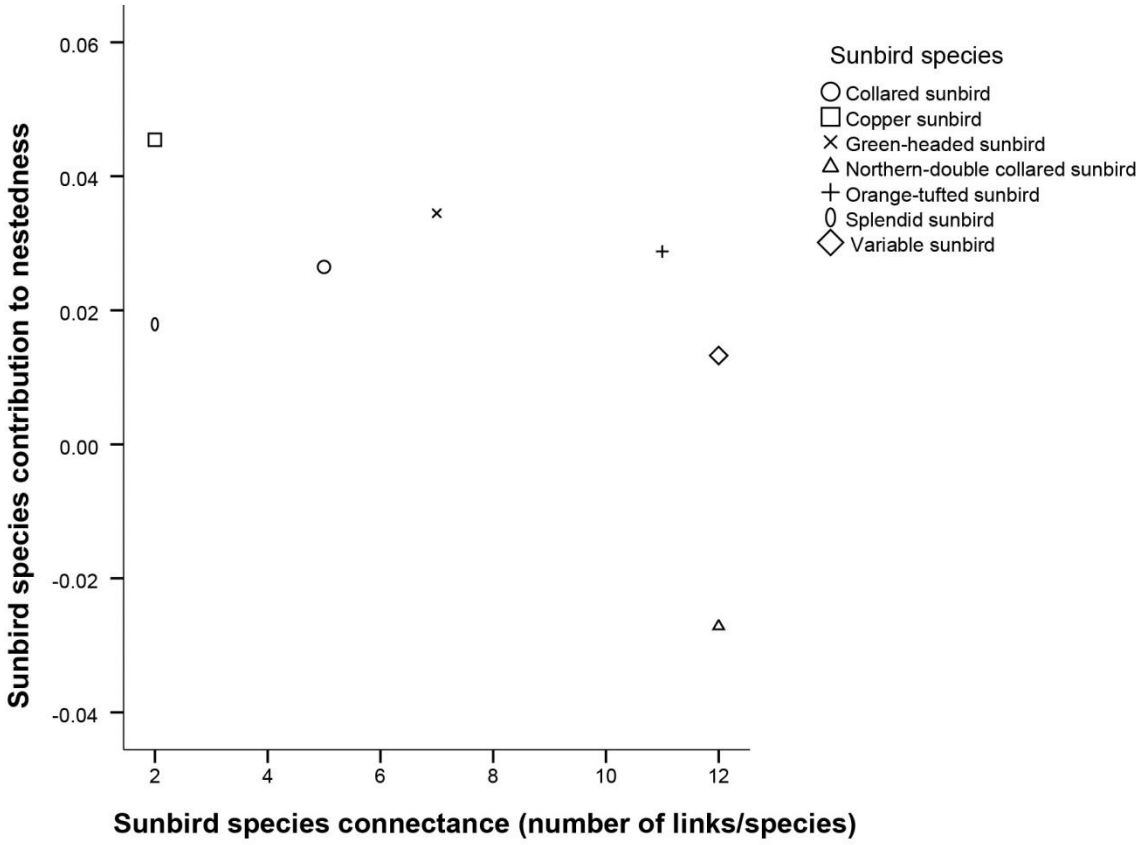
| S/N | Species | Number seen | Abundance Threshold | Category | Status |
|---|---|---|---|---|---|
| 1 | Northern-double collared sunbird | 359 | >100 | Abundant | Low Risk |
| 2 | Variable sunbird | 525 | >100 | Abundant | Low Risk |
| 3 | Orange-tufted sunbird | 356 | >100 | Abundant | Low Risk |
| 4 | Green-headed sunbird | 97 | <100 | Rare | High Risk |
| 5 | Copper sunbird | 28 | <100 | Rare | High Risk |
| 6 | Splendid sunbird | 20 | <100 | Rare | High Risk |
| 7 | Collared sunbird | 0 | <100 | Rare | High Risk |
| 8 | Pygmy sunbird | 4 | <100 | Rare | High Risk |
| 9 | Olive-bellied sunbird | 0 | <100 | Rare | High Risk |
| 10 | Olive sunbird | 0 | <100 | Rare | High Risk |
| 11 | Green sunbird | 0 | <100 | Rare | High Risk |
| | **Total** | **1389** | | | |

Appendix 5.3: Key network parameters for the flower visitation network

| S/n | Network property | Metric Value |
|---|---|---|
| 1 | Nestedness | 73.23 |
| 2 | Connectance | 0.52 |
| 3 | Number of links per species | 2.42 |
| 4 | Network size | 14 x 7 |

Appendix 5.4: The variation in level of connectance, contribution to nestedness and status category of sunbird species.

| Sunbird Species | Abundance | Status | Degree Distribution | Connectance | Contribution to nestedness |
|---|---|---|---|---|---|
| Variable Sunbird | 525 | Abundant | 12 | 0.857 | 0.013247479 |
| Northern double collared Sunbird | 359 | Abundant | 12 | 0.857 | -0.027136377 |
| Orange-tufted Sunbird | 356 | Abundant | 11 | 0.785 | 0.028770467 |
| Green-headed Sunbird | 97 | Rare | 7 | 0.5 | 0.034479057 |
| Copper Sunbird | 28 | Rare | 2 | 0.142 | 0.045443784 |
| Splendid Sunbird | 20 | Rare | 2 | 0.142 | 0.017911623 |
| Collared sunbird | 0 | Rare | 5 | 0.357 | 0.02646547 |




Appendix 5.5: The relationship between connectance (degree) and sunbird species contribution to nestedness in a flower visitation network at Ngel Nyaki.

## REFERENCES


Alarcón, R., Waser, N. M., & Ollerton, J. (2008). Year-to-Year Variation in the Topology of a Plant-Pollinator Interaction Network. *Oikos*, 117(12), 1796-1807.

Alcántara, J.M., & Rey, P.J. (2012). Linking topological structure and dynamics in ecological networks. *The American Naturalist*, 180(2), 186-199.

Almeida-Neto, M., Guimaraes, P., Guimarães, P. R., Loyola, R. D., & Ulrich, W. (2008). A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos*, 117(8), 1227-1239.

Allesina, S., & Tang, S. (2012). Stability criteria for complex ecosystems. *Nature*, 483(7388), 205-208.

Atmar, W., & Patterson, B. D., (1993). The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia*, 96(3): 373-382.

Bascompte, J., Jordano, P., Melián, C. J., & Olesen, J. M., (2003). The Nested Assembly of Plant-Animal Mutualistic Networks. *Proceedings of the National Academy of Sciences of the United States of America*, 100(16), 9383-9387.

Bascompte, J., Jordano, P., & Olesen, J. M. (2006). Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science*, 312(5772), 431-433.

Bascompte, J., & Jordano, P. (2007). Plant-animal mutualistic networks: the architecture of biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 567-593.

Bascompte, J., & Stouffer, D. B. (2009). The assembly and disassembly of ecological networks. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1524), 1781-1787.

Bastolla, U., Fortuna, M. A., Pascual-Garcia, A., Ferrera, A., Luque, B., & Bascompte, J. (2009). The architecture of mutualistic networks minimises competition and increases biodiversity. *Nature*, 458(7241), 1018-1020.

Berlow, E. L. (1999). Strong effects of weak interactions in ecological communities. *Nature*, 398(6725), 330-334.

Berlow, E. L., Neutel, A., Cohen, J. E., DeRuiter, P. C., Ebenman, B. O., Emmerson, M., . . . Kokkoris, G. D. (2004). Interaction strengths in food webs: issues and opportunities. *Journal of animal ecology*, 73(3), 585-598.

Bewick, S., Brosi, B. J., & Armsworth, P. R. (2013). Predicting the effect of competition on secondary plant extinctions in plant–pollinator networks. *Oikos*, 122(12), 1710-1719.

Bibby, C. J., Burgess, N., Hill, D., & Mustoe, S. (2000). *Bird Census Techniques*. Academic New York.

Chapman, J. D., & Chapman, H. M. (2001) *The Forests of Taraba and Adamawa States, Nigeria. An Ecological Account and Plant Species Checklist*. University of Canterbury, Christchurch, New Zealand.

Csermely, P. (2004). Strong links are important, but weak links stabilise them. *Trends in Biochemical Sciences*, 29(7), 331-334.

Csermely, P. (2009). *Weak Links as Stabilisers of Complex Systems*. 101-116.

Dormann, C.F., Fründ, J., Blüthgen, N., & Gruber, B. (2009). Indices, graphs and null models: analysing bipartite ecological networks.

Dowsett-Lemaire, F. (1989). Physiography and vegetation of the highland forests of eastern Nigeria. A preliminary natural history survey of Mambilla Plateau and some lowland forests of eastern Nigeria. Ely, Tauraco Press (*Tauraca Research Report*, 1), 6-12.

IUCN. (2012). *IUCN Red List of Threatened Species*. Version 2012.2. International Union for the Conservation of Nature Gland, Switzerland.

James, A., Pitchford, J. W., & Plank, M. J. (2012). Disentangling nestedness from models of ecological complexity. *Nature*, 487(7406), 227-230.

James, A., Pitchford, J. W., & Plank, M. J. (2013). "Disentangling nestedness" disentangled Reply. *Nature*, 500(7463): E2-E3.

Jordán, F. & Scheuring, I. (2004). Network ecology: topological constraints on ecosystem dynamics. *Physics of Life Reviews*, 1(3), 139-172.

Kaiser-Bunbury, C. N., Traveset, A., & Hansen, D. M. (2010). Conservation and restoration of plant–animal mutualisms on oceanic islands. *Perspectives in Plant Ecology, Evolution and Systematics*, 12(2), 131-143.

Lawton, J. (1990). Species richness and population dynamics of animal assemblages. Patterns in body size: abundance space. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 330(1257), 283-291.

Mace, G. M., Collar, G. M., Gaston, K. J., Hilton-Taylor, C., Akcakaya, H. R., Leader-William, N., . . . Stuart, S. N. (2008). Quantification of extinction risk: IUCN's system for classifying threatened species. *Conservation Biology*, 22(6), 1424-1442.

May, R. M. (1972). Will a Large Complex System be Stable? *Nature*, 238(5364), 413-414.

McCann, K., Hastings, A., & Huxel, G. R. (1998). Weak trophic interactions and the balance of nature. *Nature*, 395(6704), 794-798.

McCann, K. S. (2000). The diversity–stability debate. *Nature*, 405(6783), 228-233.

McQuaid, C. F., & Britton, N. F. (2013). Network dynamics contribute to structure: nestedness in mutualistic networks. *Bulletin Mathematical Biology*, 75(12), 2372-88.

Memmott, J., Waser, N. M., & Price, M. V. (2004). Tolerance of Pollination Networks to Species Extinctions. *Proceedings: Biological Sciences*, 271(1557), 2605-2611.

Montoya, J. M., Pimm, S. L., & Solé, R.V. (2006). Ecological networks and their fragility. *Nature*, 442(7100), 259-264.

Olesen, J. M., Bascompte, J., Elberling, H., & Jordano, P. (2008). Temporal dynamics in a pollination network. *Ecology*, 89(6), 1573-1582.

R Core Team. (2013). R: A language and Environment for Statistical Computing, R Foundation for statistical Computing, Vienna, Austria. http:// www.R-project.org/.

Saavedra, S., & Stouffer, D. B. (2013). "Disentangling nestedness" disentangled. *Nature*, 500(7463), E1-E2.

Saavedra, S., Stouffer, D. B., Uzzi, B., & Bascompte, J. (2011). Strong contributors to network persistence are the most vulnerable to extinction. *Nature*, 478(7368), 233-235.

Staniczenko, P. P., Kopp, J. C., & Allesina, S. (2013). The ghost of nestedness in ecological networks. *Nature communications*, 4, 1391.

Stouffer, D. B., & Bascompte, J. (2010). Understanding food-web persistence from local to global scales. *Ecology letters*, 13(2), 154-161.

Thébault, E., & Fontaine, C. (2010). Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science*, 329(5993), 853-856.

Tylianakis, J. M. (2009). Warming up food webs. *Science*, 323(5919), 1300-1301.

Tylianakis, J. M., Laliberté, E., Nielsen, A., & Bascompte, J. (2010). Conservation of species interaction networks. *Biological Conservation*, 143(10), 2270-2279.

Tylianakis, J. M., Tscharntke, T., & Lewis, O. T. (2007). Habitat modification alters the structure of tropical host–parasitoid food webs. *Nature*, 445(7124), 202-205.

Vidal, M. M., Hasui, E., Pizo, M. A., Tamashiro, J. Y., Silva, W. R., & Guimaraes Jr., P. R. (2014). Frugivores at higher risk of extinction are the key elements of a mutualistic network. *Ecology*.

# CHAPTER SIX

## Sunbird pollination and the fate of strong contributors to mutualistic network in a West African Montane Forest

### 6.0: Discussion and Summary

This chapter recaps the findings of my thesis, which examined sunbird pollination and current theories on the fate of strong contributors to a mutualistic network in a West African montane forest. This study was conducted in the Ngel Nyaki Forest Reserve, North-East Nigeria, and used contemporary methods of network analysis to investigate the consequences of species attributes such as relative abundance, contribution to nestedness, species interaction strengths and the effects these has on species and network stability. To the best of my knowledge, this is the first time in Africa that sunbirds have been exclusively studied using bipartite analysis and associated metrics.

An investigation into how changing landscapes and habitats might affect sunbird distribution and abundance at Ngel Nyaki Forest Reserve was the focus of chapter two. In chapter three, I compared a sunbird-tree visitation with a sunbird-tree pollination network to determine how good a proxy bird visitation is to bird pollination. In chapter four, I examined how species abundance influences interaction strength in a sunbird-tree pollination network at the reserve. Finally, the survival of strong contributors to the structure and stability of a sunbird-tree flower visitation network was investigated in chapter five.

The Ngel Nyaki Forest Reserve includes one of the rarest types of forests in Africa, and like most Afromontane forests is vulnerable to anthropogenic drivers of fragmentation because it occurs where human population pressure is high (Klein et al., 2007). Habitat fragmentation

has been identified as the primary cause of bird species loss (Wilcove et al., 1986; Manu et al., 2007); it is also a major global cause of species loss and changes in abundance of surviving species. Apart from species- level effects, fragmentation affects community wide interactions such as mutualistic interaction networks between plant species and their pollinators. These effects are intensified by the reduction in the size of the forest and a corresponding decline in population of various species often trapped in remnant fragments, especially sedentary species like trees. However, for sunbird species, their high mobility allows them to easily migrate or shift their range to more suitable habitats, leaving a void in their previous habitats followed by a cascade of disruptions, with the most affected group of species being plants that rely solely on biotic pollinators for their reproductive wellbeing. However, even in self-compatible species (where individuals may pollinate themselves), the shortage in pollinators could have negative consequences such as inbreeding depression, reduced fitness and increased susceptibility to external pressure, as is often the case with plant populations in small fragments. These negative effects of fragmentation often snowball into cascades of disruptions, which might eventually lead to the collapse of the entire community.

### 6.1: Changing landscapes and fragmentation: the implication for sunbird species diversity and abundance

A growing body of empirical data suggests that the stability of networks and communities over time increases with diversity (Borer et al., 2012; Tilman et al., 2001). This implies that knowledge of species diversity and abundance can mirror how various systems function or might respond to external perturbations. The relatively high diversity of sunbird species recorded in this study compared to other related studies in similar landscapes (Janeček et al., 2012; Manu et al., 2010; Sedláček et al., 2007; Waltert et al., 2005) suggest that the sunbird-

tree mutualistic network (Chapter three) would be highly productive and stable. This is because diversity and abundance promotes ecosystem multi-functionality (Maestre et al., 2012) and ensures the stability of networks through high connectance (James et al., 2012). Since highly connected species are the building blocks of a resilient network, they are intrinsically less prone to environmental disturbance (James et al., 2012). However, rare species with low connectance need a robust network of more generalised species to persist in the network (Chapter three).

Habitat selection by birds among other factors is determined by the presence of similar or closely related species (or functional guilds): this attraction to habitats already occupied by conspecifics is sometimes effected through signals such as songs or calls by conspecifics (Cody, 1985). Therefore, the wide distribution of abundant species such as northern-double collared sunbird, variable sunbird and orange tufted sunbird across the Ngel Nyaki Reserve, might serve as ecological cues for less abundant species such as collared sunbird, green sunbird, to be a part of the network. This is the principle behind nestedness (chapter three and five); the tendency for ecological specialist to interact with generalist species. This thesis therefore highlights the importance of abundance and spatial distribution in shaping network structure (nestedness), thereby promoting biodiversity (Bascompte et al., 2003).

### 6.2: Effects of fragmentation on sunbird distribution and well-being

Some mutualisms notably seed dispersal are adversely affected by fragmentation in the Ngel Nyaki forest (Aliyu et al., 2014). However, my results indicate that fragmentation poses no visible threat to sunbird pollination. Several factors support this inference:

First, despite the natural distribution of sunbird species in primary forests, most Afro-tropical sunbird species have adapted to a wide range of habitats such as city gardens, scrubland,

desert fringes, plantations, tree-lined roads, secondary growth forest and forest openings. These diverse habitats hold varying number of individuals of most species (Mann & Cheke, 2010). Although the abundance and diversity of species in these habitats varies with resource availability, the adaptation to a broad spectrum of habitat choices is an indication of the inherent resilience of sunbird species to anthropogenic changes. This view corroborates with results of chapter two, where I found no significant difference in abundance and diversity between riparian fragments and forest edge; suggesting that fragmentation is not yet a threat to the wellbeing and survival of sunbird species in the reserve.

Moreover, an ongoing assessment in the same forest reserve to investigate the effects of fragmentation on gene flow among populations of three amphibian species in riparian fragments and continuous forests revealed no significant genetic variation among populations (Arroyo unpublished data) indicating that fragmentation was yet to be a threat to gene flow. This lends further support to my conclusion that sunbird species are under no threat as a result of the present state of fragmentation, especially given their high mobility. This conclusion was made based on the distribution and abundance of sunbird species in the reserve (Chapter two).

Another factor which may contribute to the pattern of distribution of sunbird species in the reserve is the similarities in micro habitats between the fragments and the forest edge. Sunbird species are light-loving, edge tolerant and explore different forest strata based on availability of food (Mann & Cheke, 2010), which drives their preference for habitats with features typical of edge habitats, such as accessible floral resources, adequate sunlight, temperature, and high density of insects as opposed to interior (Schmiegelow & Mönkkönen, 2002). Based on personal observation, there were some similarities in vegetation structure and composition of floral resources between the riparian fragments at Ngel Nyaki and the

continuous forest edge. Both habitats expose sunbird species to the same "edge effects" which seem to have no observable negative impact on sunbird abundance. This implies that sunbird species would function optimally and persist for years in these fragments so long as the fragments continue to provide basic resources such as food and nesting sites. However, in terms of the ratio of edge to interior (i.e. habitat breadth), the forest edge habitat was clearly more extensive in breadth than the fragments. Except for locations where transects intersect, most riparian fragments were less than 100 m in breadth. Furthermore, from focal observation and transect assessments, I found that sunbird species had regular flight paths along the edges of the forest, and seldom fly breadth-wise towards the interior, suggesting that habitat breadth is most likely a less crucial habitat variable to sunbird species wellbeing. The consistent and predictable pattern of movement of sunbird species in both habitat types (riparian fragments and continuous forest) as well as the presence of similar micro-habitat features, suggests that habitat structure and resource availability could be the proximate factors controlling the distribution and abundance of sunbird species at Ngel Nyaki forest.

Knowledge of how sunbirds utilise disturbed habitats can be used to effectively manage these habitats to meet the needs of people without disrupting the process of pollination and the survival of sunbird species. The limitation, however, is that management of habitats must be integral and must include other non-avian species that occupy the same habitats or fundamental niche as sunbird species.

### 6.3: Sunbird distribution: rarity or specialisation?

Past studies have shown that not all rare species are specialist, and a real specialist does not necessarily have to be rare (Dorado et al., 2011). In most cases, rare species appear to be more specialised than they really are because rare species have a low probability of being observed, leading to an underestimate in the number of species they interact with (Dorado et

al., 2011). Although effort was made to sample as many sites as was logistically feasible in this study, the chances of observing a rare species will always be limited by a species relative abundance and its spatial distribution. In this study, some sunbird species were only sighted a few times or, in the case of green sunbird, just a single observation, during mist-netting. While it could be inferred that the distribution and abundance of some sunbird species were products of sampling artefacts (Vázquez et al., 2009), it is less likely that increased sampling effort would have resulted in any significant increase in abundance of green sunbird in the reserve. Based on this rationale and the available empirical data, I can unequivocally say that green sunbird is a rare species at Ngel Nyaki forest and not necessarily a specialist, as there is no strong empirical evidence to support any claim of specialisation based on a single interaction. Apart from rarity, other factors such as altitudinal migration (e.g. Cameroon sunbird) and preference for specific habitats (green sunbird) could limit the chances of observing some sunbird species.

### 6.4: Habitat generalisation, resource availability and the implication for network stability

Many plant –pollinator interactions are generalised (Waser et al., 1996; Waser & Ollerton, 2006). Variations in seasonal abundance and resource availability, accentuate this generalisation (Ollerton & Lack, 1998). Consequently, the structure of pollination networks changes continually as pollinators switch plant species in response to the availability of resources and plant species, attracting a changing pollinator assemblage throughout the season depending on pollinator presence. The importance of this flexibility and behavioural shifts to the stability of networks has been previously demonstrated in mutualistic networks (Basilio et al., 2006; Fortuna & Bascompte, 2006; Kaiser-Bunbury et al., 2010) and food webs (Kondoh, 2003).

The generalised pattern of spatial distribution of sunbird species at Ngel Nyaki (Chapter two) which also corresponds with the generalised flower visitation interaction pattern (Chapter three), suggest that generalist sunbird species would be flexible and amendable to seasonal changes in host abundance by switching from one available host to another, thus the sunbird-tree network structure would be seasonally variable with regards to species composition. However, the presence of a core group of highly connected generalist species would reduce the level of spatio-temporal variability in the resultant network structure. This core group of generalists and their ability to find new partners in the event of loss of original partner species to extinction supports the view that generalist pollinators play a stabilising role in network and species survival (James et al., 2012). Since network re-wiring does not only include reordering of entire interactions, but also shifts in frequencies of mutual dependence, the presence of abundant species or habitat generalists are pivotal to network stability because generalist species can maintain links with species requiring unique habitats by virtue of their generalisation and ubiquity. This reduces the number of species that would have been disconnected from the network.

For instance, abundant species in any given year are most likely to interact with a large number of partner species and function both as generalist pollinators and/or habitat generalists, while rare species by virtue of their low abundance are likely to interact with only a few partners and even less during a re-wiring process because of low encounter rate (Dupont et al., 2003; Ollerton et al., 2003; Stang et al., 2006). This implies that the core group of generalist species would be the main determinant of the temporal structure and stability of a network because of their seeming generalised distribution. However, this assertion can only be confirmed if a comparative analysis is carried out on my networks over

a time series, either yearly or seasonally; only then can conclusions be made on a species role in the spatio-temporal stability of the sunbird-tree pollination network structure.

### 6.5: Bird visitation as a proxy for bird pollination

Insects have been the focus for studies that explored the functional properties of plant-pollinator networks where flower visitation frequencies are used as proxies for pollination effectiveness (Memmott, 1999; Vázquez et al., 2012). Proxies, while not perfect (King et al., 2013) are the most feasible approach for measuring pollinator efficiency. It is extremely difficult to quantify pollination success following a single flower visit by an insect or bird. This is because pollinators can visit flowers as florivores, nectar robbers or to prey on other visitors.

The results of this study showed that only 36 % of the species (sunbird and trees) in the pollen transport network were present in the flower visitation network. The compositional difference in species between the flower visitation network (FVN) and pollen transport network (PTN) suggest that the two networks are likely to function differently. However, in chapter 3, I demonstrated congruence between FVN and PTN. The most active species were common to both networks. In fact the same species, three of the five common sunbird species accounted for about 90 % of total visits to flowers and approximately 80 % of total pollen transported. The huge contributions made by common species to both networks is enough to mute the contrasting effects of species unique to each network and explains the high positive correlation between FVN and PTN.

The fact that the FVN and PTN did not differ significantly in nestedness and connectance (Chapter three) demonstrates that nestedness and connectance are invariant to species identity but rather sensitive to species degree, relative abundance and network asymmetry (ratio of

animals to plant species in the network) (Blüthgen, 2010; Dormann et al., 2009). Nestedness and connectance are effective descriptors of network structure and the best predictors of network stability and species survival (James et al., 2012; Saavedra et al., 2011). My result indicates that nestedness and connectance, lacks the resolution for detecting significant structural differences between closely related networks such as PTN and FVN. This finding is consistent with previous studies (Alarcón, 2010; Alarcón et al., 2008).

### 6.6: Specialisation and congruence between flower visitation and pollen transport networks

From the results of my network level analysis (Chapter three), I found that the PTN was more specialised than the FVN. This finding is in consonance with those of past studies (e.g. Alarcón, 2010; Popic et al., 2013). The structural dissimilarities, evident in the difference in size and dimension of the FVN and PTN, points to the fact that, the FVN often includes antagonistic interactions such as nectar robbing, insect predation and pollen consumption (Alarcón, 2010). Unfortunately, these activities are hard to tease apart from true mutualistic interactions during focal observations since most of them involve contact with flowers and are thus described as flower visitation, increasing the level of generalisation; whereas, the PTN is a product of a direct measure of pollen recovered from the bodies of sunbirds and was more parsimonious than the FVN. Thus analyses of flower visitation networks often suggest that plants actually interacted with more potential pollinators than was the case in reality (Popic et al., 2013). A more specialised PTN as opposed to FVN is therefore an indication that the inclusion of nectar thieves, insect predators with visitors that genuinely contact flowers, leads to overestimation of the level of generalisation among species. This is why it is better to combine proxies to effectively describe a pollination system, since flower visitation

networks often overrates the structural and functional properties of networks. This is consistent with the conclusions of Popic et al. (2013), where it was revealed that although FVN and PTN may appear to be structurally similar, the function of species cannot be predicted based on a single proxy.

### 6.7: How species abundance affects interaction strength in the sunbird-tree network

Abundance is one of the most crucial first-order properties of networks, and contributes the most to the structural organisation of the network. Studies have used abundance estimates as a key predictor of a species IS (interaction strength). The concept of IS was originally developed to demonstrate how food webs are structured and to explain how biological systems are organised and sustained (Vazquez et al., 2007).

The main objective of examining the concept of IS in this thesis was to investigate how a species relative abundance determines its interaction effect or impact on other species. This per-species interaction effects was examined in terms of a species flower visitation frequency and quantity of pollen transported by each sunbird species in the network. My results confirm that species relative abundance is a major determinant of its IS. Although the efficiency of species measured through qualitative assessment such as pollen load on the bodies of sunbirds was invariant to abundance, differences in visitation rates implies that overall, abundance still affects interaction strength. Although some species were relatively stronger interactors in both networks, the strongest contributor for FVN was not the strongest for PTN. This finding is in line with the results of chapter three where I inquired whether FVN equates to PTN, and demonstrates the importance of combining proxies when evaluating pollination efficiency. In this study, the strongest contributors to the combined "pollination network" are northern-double collared sunbird (pollinator) and *Nuxia congesta* (tree). The abundance and distribution of these two species at Ngel Nyaki would be a guarantee that specialist species

despite their spatio-temporal limitations would have assurance of reproductive fitness since our strong contributors have a tendency to be encountered more often.

My result does emphasise the importance of rare species despite being often described as weak and less crucial links due to their reciprocal contributions to partners. In this study, rare species tend to contribute more to nestedness than abundant species. Moreover, the presence of rare species acts as buffers against perturbations and enhances network stability (Bascompte et al., 2006; Vazquez et al., 2007). Based on this view, and in accordance with my results, the Ngel Nyaki sunbird-tree pollination network will be stable as a result of the presence of asymmetric interactions (strong and weak links).

## 6.8: The fate of strong contributors to the structure of a sunbird-tree flower visitation network.

Understanding the stability of mutualistic networks is extremely important, because the survival of many species depends on networks of mutualistic partnership with other species; but so far, these inter-species partnerships have almost only been explored through theoretical and simulation studies. This thesis addressed this issue empirically testing theories on the relationship between extinction risk and network structure. A unique aspect of this thesis was the use of sunbird species rather than insects considering the fact that past studies had historically focused on insects (Alarcón, 2010; Alarcón et al., 2008; Memmott, 1999; Popic et al., 2013; Saavedra et al., 2011; Vázquez et al., 2012).

Although the size of my data was too small to allow for a statistically robust analysis, with regards to the difference in contribution to nestedness between rare and abundant species, it was strong enough to reveal an interesting trend. The finding that rare species contribute

more to nestedness than abundant species is noteworthy in the sense that it provides insights to why strong contributors to nestedness are thought to be the most prone to extinction. My approach of working out extinction proneness based on IUCN criteria rather than extinction simulation (as was the common practice with past studies (Saavedra et al., 2011; Stang et al., 2007; Vázquez & Aizen, 2004; Verdú & Valiente-Banuet, 2008)) provided a biologically realistic framework to test current theories and hypothesis on the fate of strong contributors to nestedness and their survival probabilities (Saavedra et al., 2011). Conversely, my findings also lend support to the tenet that a species survival probability increases with its connectance (i.e. its number of mutualistic partners) (James et al., 2012).

My result highlighted the context dependency of the term "strong contributor", and confirms that between rare and abundant species, any of the two groups or individuals in each group could be described as a strong contributor to network structure depending on the network property (e.g. nestedness, connectance or IS) under consideration. In this study, rare species contributed more to nestedness while abundant species were the most connected. My result therefore highlights the need for studies to be explicit on what is measured as a species' strength and most importantly, cautions against conclusions that presume a species identified as a weak contributor based on one parameter or metric (e.g. nestedness or connectance), is generally less- important or weak across all metrics (Berlow et al., 2004). The result of this thesis emphasises the importance of weak links (rare species), in this case strong contributors to nestedness, and strong links (abundant or highly connected species). In the light of the above, copper sunbird and northern-double collared sunbird are the most crucial species of sunbirds, in the sunbird-tree interaction network at Ngel Nyaki as they contextually represent the strongest contributors to network structure.

At Ngel Nyaki Forest Reserve my result suggest that nestedness would decrease overall with the loss of rare species. However, according to network theory, loss of rare species will not collapse the network, since it is the common species with the most interaction partners that maintain the stability of the network. One unique contribution of this study to cooperative interaction networks, is the provision of a biologically realistic reason why strong contributors to network stability are the most vulnerable to extinction. Furthermore, the finding that the loss of rare species decreases overall nestedness, lends support to the view that nestedness promotes biodiversity. Since rare species tend to contribute more to nestedness, this could be of interest to conservation biologist. However, in terms of interpreting the importance of strong contributors to network structure, connectance is a better metric than nestedness; since it is easier to relate to the reason why a species with more partners will be the least likely to go extinct. I recommend the incorporation of both properties into network models designed to address conservation issues as this would ensure that rare and abundant species are considered during conservation planning.

The result highlights the importance of each species (rare or abundant, strong or weak) in shaping and sustaining the structure of mutualistic networks. The Ngel Nyaki sunbird-tree network would be stable because theory suggests that the most resilient networks, most able to survive perturbations are composed of many weak and a few strong interactions, which enable them to enhance and optimise their intrinsic stability.

### 6.9: Conclusion

Since abundance and diversity are the main determinants of the structure of a network; by reflecting most second-order network properties such as connectance, number of links per species and to some extent nestedness, I conclude that the most abundant species from the genus *Cinnyris* are the most crucial for the sunbird-tree network structure. Therefore,

exclusion of members of the genus *Cinnyris* from the network would definitely alter the topology of the present networks or dislodge the existing links. However, since the flower visitation and pollen transport networks are generalised, there would be a horde of alternatives for surviving species to re-wire (i.e. establish new links), should there be any disruption of the mutualistic networks at Ngel Nyaki.

Finally, since generalist species are more prone to coexist with new species, as this offers more opportunity for intrinsic fitness, the generalised sunbird-tree pollination networks described in this thesis imply that there is potential for growth and expansion through addition of new species of trees-through seed dispersal and sunbirds- through range shifts to the existing sunbird-tree community at Ngel Nyaki forest. Similarly based on the level of nestedness, the Ngel Nyaki sunbird-tree pollination network would most likely support more species addition to the existing network and by extension more biodiversity.

### 6.10: General limitations of the study

Firstly, most pollen grains found on the fore-crown of sunbirds captured in mist-nets were heterospecific and requires careful observation to tease apart. Nevertheless, I was able to calculate the average amount of pollen transported in-between foraging sessions, estimated as a fraction of the total load per individual per capture, as most of the pollen was lost in transit and/or during struggle while trapped in mist-nets.

Secondly, my network was relatively smaller than many insect pollinators - plant networks that have been used to develop network theory. Consequently, a strong relationship or effect was required to achieve any statistically significant result.

Thirdly, certain flowering trees were restricted to very steep slopes and were often surrounded by dense and emergent canopy trees, making it almost impossible to observe them. This challenge would have been overcome with the construction of canopy walk-ways or strategic canopy-level observation posts. However, these measures were not feasible as each set-up requires some sort of habitat alteration.

Lastly, this study was limited by my inability to monitor focal tree species until seed-set, which prevents me from measuring the relationship between flower visitation and seed production. In addition, my observations were carried out during seasons when most tree species were flowering in other to observe as many tree species as was logistically feasible. However, this does not preclude the fact that some tree species may flower at times other than the main flowering season at Ngel Nyaki forest.

### 6.11: General Recommendations

1. Based on overall evaluation of the "pollination" network at Ngel Nyaki, I found that abundant species from the genus *Cinnyris*: northern double collared sunbird, orange-tufted sunbird, and the variable sunbird, contributed the most to IS and connectance, and served as the architectural backbone for the highly nested FVN and PTN. However, rare species such as copper sunbird and splendid sunbird, were among the strongest contributors to nestedness, and may act as buffers against the spread of external disturbance. Conservation plans that incorporate the wellbeing of this group of species would by extension protect the entire sunbird-tree network in the reserve.

2. This study identified a need for the protection of grassland habitats, since this habitat might be crucial to the reproductive fitness of most ground or grass nesters such as the

variable sunbird. I therefore recommend that burning of the Ngel Nyaki grassland habitats be controlled and whenever the need arises, regulated to fall before or after the breeding season of most grass nesters/breeders.

3. More effort should be focused on determining the actual population and distribution of rare sunbird species that were identified in this study to facilitate the protection of their unique habitats in the reserve and to boost appreciation of their role in the sunbird-tree network.

4. I recommend a year-long continuous assessment across seasons to generate a comprehensive quantitative/ qualitative data in order to expand the existing network through the inclusion of rare and migratory species of sunbirds. This networks can then be examined as motifs by comparing species assemblage at different seasons (wet and dry)

**Future Direction**

1. Future research would focus on expanding the network to incorporate other pollinator taxa such as insects and other avian families that visit flowering plants at Ngel Nyaki.

2. The development of a comprehensive network of pollinators and plants for the Mambilla plateau ecoregion.

3. Develop models that would predict ecological fragility and robustness of networks in fragmented landscapes by comparing plant-pollinator networks from different forest communities along a disturbance gradient.

## REFERENCES


Alarcón, R. (2010). Congruence between visitation and pollen-transport networks in a California plant–pollinator community. *Oikos*, 119(1), 35-44.

Alarcón, R., Waser, N. M., & Ollerton, J. (2008). Year-to-year variation in the topology of a plant–pollinator interaction network. *Oikos*, 117(12), 1796-1807.

Aliyu, B., Adamu, H., Moltchanova, E., Forget, P.M., & Chapman, H. M. (2014). The Interplay of Habitat and Seed Type on Scatterhoarding Behavior in a Fragmented Afromontane Forest Landscape. *Biotropica*, 46(3), 264-267

Bascompte, J., Jordano, P., Melián, C. J., & Olesen, J. M. (2003). The Nested Assembly of Plant-Animal Mutualistic Networks. *Proceedings of the National Academy of Sciences of the United States of America*, 100(16), 9383-9387.

Bascompte, J., Jordano, P., & Olesen, J. M. (2006). Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science*, 312(5772), 431-433.

Basilio, A. M., Medan, D., Torretta, J. P., & Bartoloni, N. J. (2006). A year-long plant-pollinator network. *Austral Ecology*, 31(8), 975-983.

Berlow, E. L., Neutel, A., Cohen, J. E., DeRuiter, P. C., Ebenman, B. O., Emmerson, M., & Kokkoris, G. D. (2004). Interaction strengths in food webs: issues and opportunities. *Journal of animal ecology*, 73(3), 585-598.

Blüthgen, N. (2010). Why network analysis is often disconnected from community ecology: a critique and an ecologist's guide. *Basic and Applied Ecology*, 11(3), 185-195.

Borer, E. T., Seabloom, E. W., Tilman, D., & Novotny, V. (2012). Plant diversity controls arthropod biomass and temporal stability. *Ecology letters*, 15(12), 1457-1464.

Cody, M. L. (1985). Habitat selection in birds. Academic Press.

Dorado, J., Vázquez, D. P., Stevani, E. L., & Chacoff, N. P. (2011). Rareness and specialisation in plant-pollinator networks. *Ecology*, 92(1), 19-25.

Dormann, C. F., Fründ, J., Blüthgen, N., & Gruber, B. (2009). *Indices, Graphs and Null Models*: analysing bipartite ecological networks.

Dupont, Y. L., Hansen, D.M., & Olesen, J. M. (2003). Structure of a plant–flower-visitor network in the high-altitude sub-alpine desert of Tenerife, Canary Islands. *Ecography*, 26(3), 301-310.

Fortuna, M. A., & Bascompte, J. (2006). Habitat loss and the structure of plant–animal mutualistic networks. *Ecology Letters*, 9(3), 281-286.

James, A., Pitchford, J.W., & Plank, M. J. (2012). Disentangling nestedness from models of ecological complexity. *Nature*, 487(7406), 227-230.

Janeček, Š., Pesata, M., Mikes, V., Patacova, E., Altman, J., Kantorova, J., . . . Brom, J. (2012). Food selection by avian floral visitors: an important aspect of plant–flower visitor interactions in West Africa. *Biological Journal of the Linnean Society*, 107(2), 355-367.

Kaiser-Bunbury, C. N., Traveset, A., & Hansen, D. M. (2010). Conservation and restoration of plant–animal mutualisms on oceanic islands. *Perspectives in Plant Ecology, Evolution and Systematics*, 12(2), 131-143.

King, C., Ballantyne, G., Willmer, P. G., & Freckleton, R. (2013). Why flower visitation is a poor proxy for pollination: measuring single-visit pollen deposition, with implications for pollination networks and conservation. *Methods in Ecology and Evolution*, 4(9), 811-818.

Klein, A. M., Vaissiere, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tschantke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, 274(1608), 303-313.

Kondoh, M. (2003). Foraging adaptation and the relationship between food-web complexity and stability. *Science*, 299(5611), 1388-1391.

Maestre, F. T., Castillo-Monroy, A. P., Bowker, M. A., & Ochoa-Hueso, R. (2012). Plant species richness and ecosystem multifunctionality in global drylands. *Science*, 335(6065), 214-218.

Mann, C. F., & Cheke, R. A. (2010). Sunbirds: *A Guide To The Sunbirds, Flowerpeckers, Spiderhunters and Sugarbirds of the World*. A&C Black.

Manu, S., Peach, W., & Cresswell, W. (2007). The effects of edge, fragment size and degree of isolation on avian species richness in highly fragmented forest in West Africa. *Ibis*, 149(2), 287-297.

Manu, S., Sunday Imong, I., & Cresswell, W. (2010). Bird species richness and diversity at montane Important Bird Area (IBA) sites in south-eastern Nigeria. *Bird Conservation International*, 20(3), 231-239.

Memmott, J. (1999). The structure of a plant-pollinator food web. *Ecological letters*, 2(5), 276-280.

Minckley, R. L., & Roulston, T. (2006). Incidental mutualisms and pollen specialisation among bees. Plant-pollinator interactions: from specialisation to generalisation, The University of Chicago Press, Chicago and London, 69-98.

Ollerton, J., Johnson, S. D., Cranmer, L., & Kellie, S. (2003). The pollination ecology of an assemblage of grassland asclepiads in South Africa. *Annals of botany*, 92(6), 807-834.

Ollerton, J., & Lack, A. (1998). Relationships between flowering phenology, plant size and reproductive success in shape Lotus corniculatus (Fabaceae). *Plant Ecology*, 139(1), 35-47.

Popic, T. J., Wardle, G. M., & Davila, Y. C. (2013). Flower-visitor networks only partially predict the function of pollen transport by bees. *Austral Ecology*, 38(1), 76-86.

Saavedra, S., Stouffer, D. B., Uzzi, B., & Bascompte, J. (2011). Strong contributors to network persistence are the most vulnerable to extinction. *Nature*, 478(7368): 233.

Schmiegelow, F. K., & Mönkkönen, M. (2002). Habitat loss and frgamentation in dynamic landscapes: Avian perspective from the boreal forest. *Ecological Applications*, 12(2), 375-389.

Sedláček, O., Reif, J., Horak, D., Riegert, J., Pesata, M., & Klvana, P. (2007). The birds of a montane forest mosaic in Big Babanki area, Bamenda Highlands, Cameroon. *Malimbus*, 29, 89-100.

Stang, M., Klinkhamer, P. G., & Van Der Meijden, E. (2006). Size constraints and flower abundance determine the number of interactions in a plant–flower visitor web. *Oikos*, 112(1), 111-121.

Stang, M., Klinkhamer, P. G., & Van der Meijden, E. (2007). Asymmetric specialisation and extinction risk in plant–flower visitor webs: a matter of morphology or abundance? *Oecologia*, 151(3), 442-453.

Tilman, D., Reich, P. B., Knops, J., Wedin, D., Mielke, T., & Lehman, C. (2001). Diversity and productivity in a long-term grassland experiment. *Science* (New York, N.Y.), 294(5543), 843-845.

Vázquez, D. P., & Aizen, M. A. (2004). Asymmetric specialisation: a pervasive feature of plant-pollinator interactions. *Ecology*, 85(5), 1251-1257.

Vázquez, D. P., Blüthgen, N., Cagnolo, L., & Chacoff, N. P. (2009). Uniting pattern and process in plant-animal mutualistic networks: a review. Oxford University Press, England, pp. 1445-1457.

Vázquez, D. P., Lomascolo, S.B., Maldonado, M. B., Chacoff, N. P., Dorado, J., Stevani, E.L., & Vitale, N.L. (2012). The strength of plant-pollinator interactions. *Ecology*, 93(4), 719-725.

Vazquez, D. P., Melian, C. J., Williams, N. M., Bluthgen, N., Krasnov, B. R., & Poulin, R. (2007). Species abundance and asymmetric interaction strength in ecological networks. *Oikos*, 116(7), 1120-1127.

Verdú, M., & Valiente-Banuet, A. (2008). The nested assembly of plant facilitation networks prevents species extinctions. *The American Naturalist*, 172(6), 751-760.

Waltert, M., Bobo, K. S., Sainge, N. M., Fermon, H., & Mühlenberg, M. (2005). From forest to farmland: habitat effects on Afrotropical forest bird diversity. *Ecological Applications*, 15(4), 1351-1366.

Waser, N. M., Chittka, L., Price, M.V., Williams, N. M., & Ollerton, J. (1996). Generalisation in Pollination Systems, and Why it Matters. *Ecology*, 77(4), 1043-1060.

Waser, N. M., & Ollerton, J. (2006). Plant-pollinator interactions: from specialisation to generalisation. University of Chicago Press.

Wilcove, D. S., McLellan, C. H., & Dobson, A. P. (1986). Habitat fragmentation in the temperate zone. *Conservation biology*, 6, 237-256.